

SERICEA LESPEDEZA (*LESPEDEZA CUNEATA*) INVASION:  
IMPLICATIONS FOR A SMALL MAMMAL COMMUNITY AND THE  
INFLUENCE OF LOCAL FIRE HISTORY

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Abstract: *Lespedeza cuneata* [(Dumont) G. Don] is a perennial legume first introduced to North America from eastern Asia in 1896 and is now widespread and well established across much of the eastern and central United States. Possible impacts of invasion and mechanisms of spread however are poorly understood. I assessed the influence of three *L. cuneata* cover classes (i.e., < 5%, 15 – 20%, and > 25% per m<sup>2</sup>) on a small mammal community in eastern Oklahoma (February 2010 to December 2011). I also examined the relationship between local fire history and *L. cuneata* cover and also considered the effect of plant invasion on the vegetation community in these same areas. My results indicate small mammal community diversity decreased with increasing *L. cuneata* cover, while *Sigmodon hispidus* body mass and catch rate increased with increasing *L. cuneata* cover. *Lespedeza cuneata* invasion decreased numbers of other species, such as *Peromyscus maniculatus*, *Neotoma floridana*, *P. attwateri*, and *Microtus pinetorum*. Model selection and multimodel inference indicated catch rates for common species were most influenced by vegetation height and occurrence of bare ground, while *L. cuneata* cover and vegetation richness exerted variable influence. For the fire history analysis, mean fire return interval (MFI) alone explained 75% of the variation in *L. cuneata* cover and the relationship was negative. Additionally, *L. cuneata* invasion suppressed graminoid cover. I provide evidence to indicate continued loss of habitat heterogeneity due to *L. cuneata* invasion will likely favor a community composed of relatively few, but individually abundant small mammal species. Findings also reveal for the first time the possible relationship between MFI and *L. cuneata* cover. My dissertation adds to the literature that indicates invasive plants are capable of modifying habitat structure and ecological conditions under which native organisms evolved.

## TABLE OF CONTENTS

Chapter	Page
I. INTRODUCTION.....	1
Literature Cited.....	6
II. EFFECT OF SERICEA LESPEDEZA ( <i>LESPEDEZA CUNEATA</i> ) INVASION ON SMALL MAMMAL COMMUNITY DYNAMICS	
Abstract.....	11
Introduction.....	12
Methods.....	15
Results.....	19
Discussion.....	23
Conclusions.....	27
Literature Cited.....	28
Tables.....	37
Figures.....	49
Appendices.....	51
III. RELATIONSHIP BETWEEN LOCAL FIRE HISTORY AND SERICEA LESPEDEZA ( <i>LESPEDEZA CUNEATA</i> ) INVASION	
Abstract.....	57
Introduction.....	58
Methods.....	60
Results.....	64
Discussion.....	67
Conclusions.....	69
Literature Cited.....	71
Tables.....	78
Figures.....	80
Appendix.....	85

## LIST OF TABLES

Table	Page
Chapter II	
Table 1. Average relative cover and standard deviation (SD) by vegetation functional group for the three <i>L. cuneata</i> cover classes sampled during the 2010-2011 small mammal survey (N = 243 for each mean). For comparison, <i>L. cuneata</i> cover is shown in italics immediately below the total mean legume cover.....	37
Table 2. Small mammals captured from February 2010 to December 2011.....	38
Table 3. Mean small mammal species richness estimates and standard deviations (SD) within three <i>L. cuneata</i> cover classes <sup>1</sup> (N = 24 for each estimate). Means did not significantly differ between cover classes ( $F = 1.124$ , $df = 2$ , $P = 0.42$ ).....	39
Table 4. Mean small mammal diversity (H') values and standard deviations (SD) by <i>L. cuneata</i> cover class <sup>1</sup> (N = 3 for each index value). Similar mean values are denoted by shared uppercase letters (Tukey's HSD $P > 0.05$ ).....	40
Table 5. Akaike's second-order information criterion (AICc) results for <i>S. hispidus</i> catch models ( $\Delta AICc \leq 7$ ).....	41
Table 6. Akaike's second-order information criterion (AICc) results for <i>P. leucopus</i> catch models ( $\Delta AICc \leq 7$ ).....	42
Table 7. Akaike's second-order information criterion (AICc) results for <i>P. maniculatus</i> catch models ( $\Delta AICc \leq 7$ ).....	43
Table 8. Results of AIC-based model averaging procedure for <i>S. hispidus</i> catch rates. Models with a $\Delta AICc \leq 7$ and free of pretending variables (Anderson 2008) were used to generate coefficient estimates.....	44
Table 9. Results of AIC-based model averaging procedure for <i>P. leucopus</i> catch rates. Models with a $\Delta AICc \leq 7$ and free of pretending variables (Anderson 2008) were used to generate coefficient estimates.....	45

Table	Page
Table 10. Results of AIC-based model averaging procedure for <i>P. maniculatus</i> catch rates. Models with a $\Delta AICc \leq 7$ and free of pretending variables (Anderson 2008) were used to generate coefficient estimates.....	46
Table 11. Relative importance of the eight predictor variables, plus the interaction term, for the species model sets. Results were determined using Akaike's second-order information criterion (AICc).....	47
Table 12. Mean weights (g), total captured, and standard deviation (N, SD) for <i>S. hispidus</i> trapped from three differing <i>L. cuneata</i> cover classes <sup>1</sup> . Similar mean weights are indicated by shared uppercase letters (Tukey's HSD $P > 0.05$ ).....	48
 Chapter III	
Table 1. Mean fire return interval (MFI; years), related descriptive statistics, and vegetation characteristics for the nine Camp Gruber study plots.....	78
Table 2. Correlation coefficients and associated <i>P</i> values for the relationships between mean <i>L. cuneata</i> cover estimates and vegetation and ground cover data. Significant <i>P</i> values ( $\leq 0.05$ ) are indicated in <i>bold italics</i> .....	79

## LIST OF FIGURES

Figure	Page
Chapter II	
Figure 1. Map of Camp Gruber vicinity (a) and small mammal sampling plots (b).....	49
Figure 2. Total counts by season and <i>L. cuneata</i> cover for <i>S. hispidus</i> (HCR [hispid cotton rat]; a), <i>P. maniculatus</i> (DM [deer mouse]; b), and <i>P. leucopus</i> (WFM [white footed mouse]; c) trapped at Camp Gruber from February 2010 to December 2011...	50
Chapter III	
Figure 1. Map of Camp Gruber vicinity (a) and <i>Q. stellata</i> and vegetation sampling plots (b).....	80
Figure 2. Fire history chart for the nine Camp Gruber study plots combined by <i>L. cuneata</i> cover class. Each horizontal line represents an individual <i>Q. stellata</i> sampled, while the dark vertical lines represent recorded fire events.....	81
Figure 3. Mean number of fires per decade within the three tested <i>L. cuneata</i> cover classes with 5% standard error bars.....	82
Figure 4. Relationship between mean <i>L. cuneata</i> (LECU) cover observed in test plots and the corresponding plot mean fire return interval (MFI). The proportional <i>L. cuneata</i> variable was arcsine transformed prior to analysis. ....	83
Figure 5. Relationship between mean fire return interval (MFI) and mean graminoid (a), shrub (b), and forb (c) cover. The proportional dependent variables were arcsine transformed prior to analysis.....	84

## CHAPTER I

### INTRODUCTION

Spatial and temporal variation exerts continual influence on biota (Axelrod 1985; Scholes and Archer 1997). In recent history however anthropogenic influences (either direct or indirect) have been identified as responsible for alteration of environmental feedbacks and resulting ecosystem change (Archer et al. 1988). For example, prior to 1940 oak-hickory forests in the eastern United States were classified as chestnut-oak. Following introduction of the invasive chestnut blight fungus (*Cryphonectria parasitica*), the system was pushed beyond its ability to recover and loss of a major biotic assemblage followed. Prior to the fungus, the American chestnut (*Castanea dentata*) occupied about 25% of the canopy in the eastern United States; however, invasion resulted in the loss of nearly all mature trees and those that remain exist only as understory sprouts that seldom survive long enough to reach sexual maturity due to persistence of the blight in the system (Paillet 2002). Removal of the chestnut has resulted in advancement of once less dominant tree species (e.g., chestnut oak [*Quercus prinus*] and red oak [*Q. rubra*]) and subsequent alteration of animal populations inhabiting the affected areas due to mast production loss in the new oak-dominated forests compared to those dominated by American chestnut (Diamond et al. 2000; Foster et al. 2002a; Foster et al. 2002b). In this



instance, invasive introduction resulted in significant economic impact, not to mention long-term effect on many ecosystem processes (Ellison et al. 2005).

While not all species introductions threaten ecosystems, each introduction event has the potential to cause dynamic shifts within the affected area. The ability of invasive species to take advantage of opportunities and cause significant ecosystem alteration is well documented (e.g., Masters and Sheley 2001; Briske et al. 2006; Ricklefs 2006). Only through diligent evaluation can we begin to understand the ramifications of invasive species introductions, which is critical for developing management strategies to mitigate effects in impacted areas or protect areas yet to be invaded.

*Lespedeza cuneata* [(Dumont-Cours.) G. Don] is native to eastern Asia and was first introduced to North America in 1896 by the North Carolina Agriculture Experiment Station due to the plant's ability to grow on nutrient poor soils (Davison 1941). The plant was not widely used until 1924 when a second introduction occurred at the Arlington Experiment Farm for soil stabilization, forage, and hay crop production (Eddy and Moore 1998). Additional introductions occurred across the Midwestern United States through the 1930s when the plant's ability to grow in poor soils and drought tolerance made it a favorite among state and federal agencies for soil conservation plantings (Ohlenbusch et al. 2007; Cummings et al. 2007). *Lespedeza cuneata* is listed as a noxious weed only in Colorado and Kansas though it is now widely distributed throughout much of the central, southeastern and eastern United States and into portions of Canada (USDA 2013).

As with other invasive species, spread of *L. cuneata* in many instances has been unintentional. One such example occurred when fields contaminated with *L. cuneata* were among those harvested for native grass seed and planted elsewhere on former farm

fields being rehabilitated under the Conservation Reserve Program (Ohlenbusch et al. 2007). However, *L. cuneata* seeds are still widely available commercially and marketed for various purposes such as soil stabilization, perceived wildlife benefit, forage and hay production. The current *L. cuneata* genotype differs from the plant's ancestral origins due to herbivore and pathogen release, as well as relatively new selective pressures that favor colonization traits (Beaton et al. 2011).

Native congeners do co-occur throughout much of the affected range, but *L. cuneata* is easily distinguished from these by terminally pointed small club shaped leaves (25-mm x 6-mm) growing on long coarse stems up to 2-m in length. All *Lespedeza* species flower from July to October and produce both chasmogamous and less conspicuous cleistogamous flowers that are obligately self pollinated (Woods et al. 2009). Propagation occurs also from vegetative buds, but the primary reproductive mechanism is likely prolific seed production, which may exceed rates well over 1,000 of the small (~ 0.2 cm) oval seeds per ramet (Fechter 2003). Seeds can germinate within 4 to 5 weeks and do best with scarification, which can occur from exposure to fire or the digestive process following grazer consumption (Blocksome 2006). The plant establishes an extensive seed bank that likely allows *L. cuneata* an extended ability to overwhelm other plant species (Williamson 2001).

Despite the potential fecundity and co-occurrence with native North American lespedezas (*Lespedeza* spp.), reports of hybridization between the invasive and native species are mixed. Hanson and Cope (1955) reported failure to produce hybrids in the laboratory, but later reported discovery of vigorous *L. cuneata* crosses with native congeners in the southeastern United States near co-occurring stands (Clewell 1967)

despite mismatched chromosomal number between the invasive *L. cuneata* ( $n = 19$ ) and the native *Lespedeza* species ( $n = 10$ ; Clewell 1966). However, no recent studies have addressed hybridization and this is an area where more research is needed.

*Lespedeza cuneata* is noted for being highly tolerant of variable growing conditions. Shade tolerance is high (Lin et al. 2004) and *L. cuneata* is also capable of modest nitrogen fixation through rhizobial colony formation on root structures (Lynd and Ansmna 1993). The plant resprouts readily following removal of aboveground growth, regardless if the disturbance was mechanical, from fire events, or otherwise. This adaptation is largely due to perennating buds protected just below the soil surface (Emry 2008) and suggests the plant evolved with frequent disturbance regimes, though information about selective pressures in the plant's native range (i.e., eastern Asia) is lacking from the published literature. Allred et al. (2009) provided further evidence of the plants broad tolerance by reporting higher seasonal leaf surface areas and photosynthetic efficiency for *L. cuneata* compared to that of native grasses, which aids in resource acquisition and competitive exclusion. Collectively these studies indicate the plant's range of adaptability to different conditions.

Herbivore avoidance due to unpalatable tannin levels likely enhances *L. cuneata* invasion potential; however, biomass levels can be decreased through manipulation of the fire-grazing interaction and subsequent exploitation of post-fire resprouts and seedlings by livestock (e.g., Cummings et al. 2007; Bell 2012). Comparatively little is known of *L. cuneata* browsing rates in wild systems, though elk (*Cervus elaphus*) have been reported to consume *L. cuneata* when the plant is present (Schneider et al. 2006; Conrad and Gipson 2012). However, insect herbivory simulations with *L. cuneata* have indicated

that even with high leaf loss effects on plant survival would be minimal and likely do little to reduce high seed production and population growth rates (Schutzenhofer and Knight 2007; Schutzenhofer et al. 2009).

Reports of possible impacts of *L. cuneata* invasion on small mammal communities are limited, but shifts in dominant vegetation have exerted negative influences (Schweiger et al. 2000; Denslow and Hughes 2004). Small mammals fill niches as herbivores, detritivores, and seed dispersers for many plant species (Bayne and Hobson 1998) and serve as important prey items for birds and other mammals (e.g., McGowan and Bookout 1986). Additionally, small mammals are important nutrient sources for carrion beetles, such as the endangered American burying beetle (Holloway and Schnell 1997), while their burrowing activity benefits soil structure and composition (Clark et al. 2005). Both directly and indirectly, small mammals are a critical component of functioning ecosystems and alterations in their abundance and distribution have the potential to greatly affect a variety of dependent processes.

The invasive *L. cuneata* poses a potentially serious threat to much of the United States and recent estimates place about 61% of the total land area (including parts of Alaska and Hawaii) at risk for eventual invasion (USDA 2012). The potential harm of this invasive plant is just now being realized and advanced through evaluation of specific biotic responses. For this reason, I chose to focus my research in the previously unexplored areas of 1) the potential influence of *L. cuneata* invasion on a small mammal community and 2) the relationships between *L. cuneata* cover and local fire history and vegetation functional groups.

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## CHAPTER II

### EFFECT OF SERICEA LESPEDEZA (*LESPEDEZA CUNEATA*) INVASION ON SMALL MAMMAL COMMUNITY DYNAMICS

#### **Abstract**

Invasive plants are capable of modifying habitat structure and a number of dependent processes. Influence on biota can be variable and often determined by species-specific traits, such as phenotypic plasticity and environmental tolerance. *Lespedeza cuneata* [(Dumont) G. Don] is a perennial legume first introduced to North America from eastern Asia in 1896 and is now widespread across much of the eastern and central United States. Possible impacts of invasion on small mammals however are poorly understood. I examined the influence of differing *L. cuneata* cover on small mammal community characteristics and on *Sigmodon hispidus* body mass. For this, I live-trapped small mammals during 2010 and 2011 at nine sample plots (1.4-ha each) situated in one of three mean *L. cuneata* cover classes (< 5%, 15 – 20%, and > 25% per m<sup>2</sup>). I also collected detailed vegetation, canopy height, and ground cover data from the 9 sample plots. Graminoid cover and small mammal community diversity decreased with increasing *L. cuneata* cover, while *Sigmodon hispidus* body mass and catch rate increased with increasing *L. cuneata* cover. Additionally, *L. cuneata* invasion decreased numbers

of other species, such as *Peromyscus maniculatus*, *Neotoma floridana*, *P. attwateri*, and *Microtus pinetoru*. Model selection and multimodel inference indicated catch rates for common species were most influenced by vegetation height and occurrence of bare ground, while *L. cuneata* cover and vegetation richness exerted variable influence. I provide evidence to indicate continued *L. cuneata* invasion will likely further reduce habitat heterogeneity and favor a less diverse small mammal community composed of relatively few, but individually abundant species.

## **Introduction**

Seemingly every suitable habitat is host to introduced organisms that evolved elsewhere under differing selective pressures. Species introductions coupled with variation and anthropogenic influence will likely drive future biodiversity to unseen levels of alteration and potential realignment (Vitousek et al. 1996; Walther et al. 2002; Hooper et al. 2012). These rapid changes in diversity and community composition are complicating assessment of impacts, not to mention confounding previous concepts of habitat restoration and management.

The majority of published accounts document negative effects of invasive species on native fauna (e.g., Vitousek 1990; Mack et al. 2000; MacDougall and Turkington 2005). However, in some cases, invasive species may become integral ecosystem components (Hobbs et al. 2006). For example in the southwestern United States, invasive saltcedar (*Tamarix* spp.) provides up to one-third of the suitable nesting habitat for the federally endangered willow flycatcher (*Empidonax traillii*) (Durst et al. 2007). Similarly, mutualistic relationship between invasive honeysuckle (*Lonicera* spp.) and

important native frugivores have been described (Gleditsch and Carlo 2011). These examples illustrate how some native fauna have adapted to and on rare occasion, benefitted from species introductions. The range of positive and negative effects highlights the need for careful evaluation of associated risks and benefits well before implementation of invasive species management plans or control efforts (Stohlgren and Schnase 2006). This is especially important as some restoration efforts intended to eliminate invasive species have had the opposite affect and only enhanced invasions due to resource release and decreased competition with native species (Minchinton and Bertness 2003). Rinella et al. (2009) described one such occurrence following herbicide treatment intended to reduce leafy spurge (*Euphorbia esula*) invasion on Montana rangeland, which resulted in long-term suppression of two native varieties over 16 years while *E. esula* frequency matched that of non-treatment plots after only 4 years.

*Lespedeza cuneata* (Dumont-Cours.) G. Don (Sericea lespedeza) is an invasive perennial legume first introduced to North America from eastern Asia in 1896 (Davison 1941). The plant forms clumps of slender woody ramets capable of growing over 1-m tall, which are lined with numerous small club-shaped leaves. As a shade tolerant plant, *L. cuneata* is capable of invading both woodlands and grasslands and the plant readily establishes on nutrient poor, disturbed soils (Davison 1941; Mays and Bengston 1985; Remaley 1998; Eddy 1999). Despite the 1896 introduction, *L. cuneata* was not widely distributed until the 1930s when it became popular among state and federal agencies for soil conservation, wildlife benefit, and forage plantings (Ohlenbusch et al. 2007; Cummings et al. 2007). *Lespedeza cuneata* is now widely distributed throughout much of the central, southeastern and eastern United States and into portions of Canada (USDA

2013). Spread has been hastened by allelopathy, high detrital deposition, high seed production, and formation of dense monospecific stands (Dove and Zipper 1997; Eddy 1999; Kalburtji et al. 2001; Cummings et al. 2007).

Many unknowns exist regarding the potential influence of *L. cuneata* invasion on ecosystem processes, especially concerning ecological thresholds (i.e., the point at which a relatively small change can result in rapid ecosystem change). Evidence does suggest however that *L. cuneata* invasion reduces invertebrate and plant diversity (Dove and Zipper 1997; Eddy 1999). Important ecosystem services are also at risk for modification (Pejchar and Mooney 2009). For example, *L. cuneata* can alter soil nutrient and carbon cycling rates (Kardol et al. 2010), as well as disrupt important plant-pollinator dynamics (Woods et al. 2011). However, knowledge of possible effects of *L. cuneata* invasion on small mammal communities is comparatively lacking. An understanding of possible negative impacts is needed because small mammals fill important ecological roles as herbivores, detritivores, and seed dispersers for many plant species (Bayne and Hobson 1998) and serve as important prey items for larger predators, such as birds and other mammals (e.g., McGowan and Bookout 1986). Small mammals also perform important ecosystem services by beneficially modifying soil structure and chemical composition through burrowing activity (Hole 1981) and nitrogen enrichment (Clark et al. 2005). Both directly and indirectly, small mammals are a critical component of functioning ecosystems and any alterations in their abundance, community composition, or both have the potential to greatly affect a variety of dependent processes.

My study objectives were to 1) evaluate the effect of different levels of *L. cuneata* cover on the ecologically important small mammal community using effects on richness,

diversity and relative abundance as metrics and 2) assess the possibility that *L. cuneata* provided more favorable conditions for the herbivorous *S. hispidus* than those available in less invaded areas by comparing body mass among *L. cuneata* cover classes.

## **Methods**

*Study site* - Camp Gruber Training Center (CGTC) and the Cherokee Wildlife Management Area (CWMA) exist as the largest contiguous tract of publicly owned land in northeastern Oklahoma. Together, the two properties total 25,868-ha of various habitat ranging from wetlands, ephemeral and permanent streams, to cross timbers, prairies and savannas (Howard 2011). About 64% (8,553-ha) of the CGTC and 86% (10,752-ha) of the CWMA consist of woody vegetation, while the remainder of both are grasslands or savannas (4,812-ha and 1,750-ha, respectively), as determined from digitization of 2011 aerial photography in a geographic information system and previous reports by Woolf and Miller (2009).

The site is relatively pristine, as evidenced by a large remnant population of the endangered American burying beetle (*Nicrophorus americanus*; Lomolino et al. 1995) and compared to other similar areas, impacts of military training at CGTC are comparatively low because the presence of the endangered beetle limits off road and ground disturbing activities (USFWS Biological Opinion #2-14-92-F-658). The area also supports a wide diversity of plants and animals, along with populations of white-tailed deer (*Odocoileus virginianus*), wild turkey (*Meleagris* spp.), bobwhite quail (*Colinus virginianus*), squirrel (*Sciurus* spp.), cotton-tailed rabbit (*Sylvilagus floridanus*), and a small herd of elk (*Cervus elaphus*).

Agriculture was the most prevalent use of the site from settlement until government acquisition began in 1935 (Howard 2011). Between 1936 and 1942, the United States Department of Agriculture enacted the Eastern Oklahoma Cookson Hills Forestry, Fish, and Game Project, which turned much of present day CGTC into a wildlife management and recreation area (U.S. Forest Service 1977). Camp Gruber opened on 12 May 1942 and served as a primary infantry and support group training base for the U.S. Army until deactivation on 3 June 1947. Military use of the Muskogee County portion resumed in 1977 when the Oklahoma Army National Guard took control of the site and has progressively increased since.

*Small mammal trapping* - I trapped small mammals using Sherman live traps (7.6 x 8.9 x 22.9-cm) seasonally during 2010 and 2011 at nine sample plots (1.4-ha each) situated in one of three mean *L. cuneata* cover classes (< 5%, 15 – 20%, and > 25% per m<sup>2</sup>) (Figure 1). The spring samples were concluded in March, the summer in June, the fall in October, and the winter in December, while plot locations were based primarily on results from previous vegetation surveys conducted at the site by Woolf and Miller (2009) and visual assessment of color aerial photography collected in 2011. Specifically, I used the 2009 vegetation survey to identify plot locations within the specified *L. cuneata* cover class ranges and used the aerial photography to control for tree canopy cover by visually comparing these locations. This approach allowed me to situate plots to best isolate the potential effects of the three varying levels of *L. cuneata* on small mammals while limiting other influential variables such as *J. virginiana* presence, woody canopy closure, and proximity to riparian habitat, all of which have been reported to alter small mammal community composition and structure (Thurmond and Miller 1994;

Schweiger et al. 2000; Horncastle et al. 2005; Matlack et al. 2008). Additionally, I considered plot accessibility, similarity of topology and terrain (using 1:24,000 USGS topographic maps), as well as other pertinent factors unique to an active military training site such as firing range surface danger zones, security restricted areas, and proximity to areas likely to contain unexploded ordinance.

During each of the eight sampling events, I trapped small mammals over four consecutive nights within plot groups, (i.e., southern plot group, mid group, and northernmost plot group). Traps were evenly placed at 15-m intervals in a 9 x 9 grid arrangement (81 traps per plot), for a total sample area of about 4.3-ha in each of the three *L. cuneata* cover categories. A previous small mammal inventory at the site indicated that *Peromyscus leucopus*, *P. maniculatus*, and *S. hispidus* were the most common species (Schnell 2006), which influenced my trap spacing and resulted in about seven traps within the home ranges of each (i.e., 0.15-0.2 ha for *P. leucopus*, *P. maniculatus*, and *S. hispidus*) (Storer et al. 1944; Jacquot and Vessery 1995; Slade and Swihart 1983).

I baited traps with rolled oats and salted sunflower seeds (4:1 ratio by weight). Captured animals were identified by species, sexed, and marked by toe-clipping. In addition, I also weighed all *S. hispidus* specimens as previous investigations at the site indicated weights for this species were possibly influenced by *L. cuneata* presence (i.e., Schnell 2006). All captured animals were handled in accordance with the Oklahoma State University animal care and use committee guidelines (Animal Care and Use Protocol (ACUP) No: AS-09-15).



*Vegetation and habitat* - I collected detailed vegetation community data from each small mammal sampling plot on 12-21 September 2011 for use as predictor variables. In summary, vegetation community characteristics and habitat variables were recorded at each of the nine sample plots (1.4-ha each) using 1-m<sup>2</sup> rigid quadrats (polyvinylchloride construction) systematically placed at 15-m intervals. At each placement, relative plant cover was visually estimated by species. In addition to the quadrats, I surveyed four randomly selected 4-m wide by 135-m long linear transects to categorize ground cover (0.5-m intervals) within each of the nine sample plots. This was done by lowering a rod (1.0-cm diameter) vertically to one side of the transect and categorizing intersected ground conditions. Vertical canopy height was measured above the ground cover point to a maximum of 8.5-m high. As with the quadrats, all linear transects were situated along north-south axes and were centered on small mammal trap lines. *Statistical analysis* – I examined the influence of mean *L. cuneata* plot cover (relative percent calculated using all plot quadrats) on seasonally pooled small mammal species richness using repeated measures analysis of variance (rm-ANOVA). I used the same rm-ANOVA design to evaluate variation in mean *S. hispidus* weights between *L. cuneata* cover classes, as well as to evaluate variation between *L. cuneata* cover classes and mean small mammal diversity, which I assigned using the Shannon-Weiner index ( $H'$ ). All significant findings (i.e.,  $P \leq 0.05$ ) were followed with Tukey's HSD to identify differing means.

I selected Poisson regression to examine the relationship between unique count data for the three most commonly captured species (*S. hispidus*, *P. leucopus*, and *P. maniculatus*) and the variables measured during the vegetation and habitat sampling.

Additionally, I included an interaction term between *L. cuneata* cover and collection season to better allocate residual error deviance because small mammal communities often vary seasonally (e.g., Deitloff et al. 2010) and omitting this possible source of variance could result in poor model fit (Kuehl 2000). Candidate models for each of the three common species were ranked according to relative support as indicated by Akaike weights ( $w_i$ ) using the AICc function of package MuMIn (version 1.9.5; Barton 2013) (Burnham and Anderson 2002). I evaluated Akaike weights to determine the relative importance of each independent variable and calculated weighted average estimates for each independent variable using a broad subset of “top” models ( $\Delta\text{AICc} \leq 7$ ; Burnham et al. 2011). Pretending variables were identified following Anderson (2008) and I excluded these from the model selection and ranking process. Variables were screened for parametric assumptions and multicollinearity was declared if correlation between predictors exceeded 0.50 (Grewal et al. 2004).

## Results

*Vegetation sampling* – I identified 157 taxa during the vegetation surveys (see Appendix A) and most overhead canopy estimates were less than 2.0-m in height (see Appendix B). Plant richness among plots ranged from 42 to 68 species (plot A and plot I, respectively). Graminoids were the most dominant functional vegetation group among the 729 total quadrats sampled, but their relative cover decreased with increasing legume cover, which consisted mostly of *L. cuneata* (Table 1). Similarly, shrub cover also decreased with increasing *L. cuneata* cover. Despite these variations in relative cover among functional groups and *L. cuneata* cover classes, the large standard deviations, with

the exception of *L. cuneata* in the high-cover plots, indicate the lack of spatial dominance for any one functional group within trapping locations.

*Small mammals* – I trapped 1,398 individuals, representing ten species, from February 2010 to December 2011. Total effort consisted of 23,044 trap nights out of a possible 23,328. Two-hundred eighty-four traps malfunctioned due to reasons ranging from scavenger disturbance, animal escape, to completely missing traps. Overall probability of capture (i.e., trap success) for all species combined was 5.4%.

*Peromyscus leucopus* was most common (N = 434), followed by *S. hispidus* (N = 419), and *P. maniculatus* (N = 338). *Reithrodontomys fulvescens* was also fairly common (N = 136); however, I trapped few *Blarina hylophaga* (Elliot's short-tailed shrew; N = 2), *R. humulis* (eastern harvest mice; N = 3), or *Microtus pinetoru* (woodland voles; N = 4) (see Table 2 for others). *Sigmodon hispidus*, *P. maniculatus*, *P. leucopus*, and *R. fulvescens* were ubiquitous and trapped at each plot and cover class sampled. In contrast, I trapped *R. humulis*, *N. floridana*, *P. attwateri*, and *M. pinetoru* only from low- and mid-cover *L. cuneata* plots.

Overall mean species richness was highest in the mid-cover class and lowest in the high-cover class, but differences were not statistically significant ( $F = 1.124$ ,  $df = 2$ ,  $P = 0.42$ ) (Table 3); however, small mammal diversity ( $H'$ ) significantly differed among *L. cuneata* cover classes ( $F = 7.43$ ,  $df = 2$ ,  $P = 0.02$ ) and the Tukey's HSD procedure indicated the high-cover mean diversity, which was the lowest observed, differed significantly from both the low- and mid-cover value means (Table 4). Catch rates were variable among the *L. cuneata* cover classes, with 64% of all *S. hispidus* (N = 268) trapped in high-cover plots, while low-cover collections accounted for about 16% (N =

67). The remaining 20% (N = 84) were captured in mid-cover plots (Figure 2a). The overall *P. maniculatus* catch was similar in low- and mid-cover plots during the study period (N = 138 and N = 141, respectively). High-cover plots accounted for about 17.5% (N = 59) of the *P. maniculatus* trapped (Figure 2b). *Peromyscus leucopus* was the most evenly caught small mammal among the *L. cuneata* cover classes (Figure 2c).

*Reithrodontomys fulvescens* was most commonly trapped from low cover plots (N = 68), though catch was similar between mid- and high covers (N = 38 and 30, respectively).

Multiple regression models were used to examine the influence of biologically relevant predictor variables on catch rates for each of the three most common small mammal species. I originally considered a pool of eleven possible predictor variables, but unacceptable levels of multicollinearity narrowed the valid predictors to eight plus the interaction term between *L. cuneata* cover class and collection season. Variables eliminated included mean count of tree litter point intercepts, and percent of vegetation within plots between 1.01 to 1.5-m and 1.51 to 2.0-m high, while the eight variables retained included collection season (i.e., winter, spring, summer, and fall coded in the analysis as a “dummy” variable); total plot vegetation species richness; percent of vegetation within plots between 0.1 to 0.5-m and 0.51 to 1.0-m high (arcsine transformed); mean count of bare ground, grass litter, and rock and gravel point-interceptions within plots; and *L. cuneata* cover class (coded as a “dummy” variable). The eight predictors plus the interaction term provided five-hundred-twelve possible model combinations ( $2^9 = 512$ ).

The AICc procedure indicated the full model minus the rock/gravel intercept, season, and interaction variable as the best to explain *S. hispidus* catch and the selected

model was 4.4 times more likely to explain catch than the next best model (Table 5). For *P. leucopus*, the full model minus only the total vegetation richness variable was selected as the top model and this model was 7.1 times more likely to explain catch than the 2<sup>nd</sup> best model (Table 6). The top model for *P. maniculatus* catch excluded mean *L. cuneata* cover class, rock/gravel, total vegetation richness, and the interaction term between *L. cuneata* cover class and season and was 2.6 times more likely to explain catch than the 2<sup>nd</sup> best model (Table 7).

Shared plausibility among possible “best” models necessitated multimodel averaging for each common species (Tables 8, 9 and 10). Averaged models indicated significant positive influence of the bare ground variable on mean catch rates while influence of both vegetation height variables was negative for each of the three common species. The grass litter variable was a significant predictor for each of the common species, although effects were positive only on *S. hispidus* catch. Similarly, *L. cuneata* cover class exerted positive influence on *S. hispidus*, while the influence of this variable on both *P. maniculatus* and *P. leucopus* catch was insignificant. The total plot vegetation richness variable was significant only for *S. hispidus* and the relationship was negative, while I detected a significant interaction between *L. cuneata* cover class and season only for *P. leucopus* catch (see Figure 2c).

Relative variable importance differed slightly among the three common species; however, common to each was the high relative importance of the bare ground, grassy litter, and both vegetation height variables (Table 11). The mean *L. cuneata* cover class variable was important only for *P. leucopus* and *S. hispidus*. In both the *P. maniculatus* and *P. leucopus* models, the season variable was highly important, but was of little

importance for the *S. hispidus* catch models ( $W = 0.16$ ). Importance of the rock/gravel variable was low and similar for *S. hispidus* and *P. maniculatus*, but of slightly higher importance for *P. leucopus*. Total plot vegetation richness was most influential in the *S. hispidus* models and had essentially no influence in models for the other two species. The interaction term between *L. cuneata* cover class and season was only important for *P. leucopus* models.

*Sigmodon hispidus* mean weights significantly varied between the three *L. cuneata* cover classes ( $F = 34.23$ ,  $df = 1$ ,  $P < 0.001$ ). The Tukey's procedure indicated the mean weights were similar for the low- (< 5%) and mid-level (15 – 20%) *L. cuneata* cover classes. Means weights for the high cover class were greater than the low- and mid-class weights (Table 12).

## **Discussion**

Interactions between plant and animal communities have received much consideration, especially in terms of potential responses to climate change (e.g., Walther et al. 2009; Schweiger et al. 2010; Bellard et al. 2012). Concern is well placed since vegetation characteristics are among primary determinants of habitat quality (Morrison et al. 2006; Monamy and Fox 2010) and shifts in plant community composition may disrupt ecological processes tied to plants, animals, or plant-animal interactions (Lyon et al. 2000). Invasive plants may further alter important processes such as mutualistic networks and ecosystem services (Pejchar and Mooney 2009; Schweiger et al. 2010). Though variation in plant composition may influence all coincident fauna, groups such as small mammals with their limited home ranges and high energetic demands will likely be

among those most affected, especially since their communities display strong ties to local vegetation structure (e.g., Kelt et al. 1994; Fox and Fox 2000). However in my study, even within the higher *L. cuneata* cover plots, *L. cuneata* cover was not spatially uniform, as evidenced by the high standard deviation values for mean cover. This variation in the vegetation community may have allowed small mammal species to persist within the spatial extents I sampled as effects of plant invasion are often most pronounced at the smallest relative scales of measurement (Powell et al. 2011). As *L. cuneata* invasion progresses this may change due to loss of habitat heterogeneity, which is a contributing factor to small mammal diversity (Groves and Steenhof 1988; Fuhlendorf et al. 2010). Even at the current level of invasion at the study site, I detected alterations in the small mammal community attributable to *L. cuneata* invasion.

Increased *L. cuneata* cover reduced small mammal diversity by creating conditions that excluded *R. humulis*, *N. floridana*, *P. attwateri*, and *M. pinetorum*; however, invasion favored other species, such as *S. hispidus*. For *S. hispidus*, *P. maniculatus*, and *P. leucopus*, consideration of habitat preferences and life histories at least partially explained some variation in catch rates. *Peromyscus maniculatus* prefers grasslands and remnant prairies within the region (Kaufman and Fleharty 1974; Schweiger et al. 2000) and graminoid suppression by *L. cuneata* in high-cover plots may have created unfavorable conditions for this regional grassland species. *Peromyscus leucopus* numbers however were consistent across tested *L. cuneata* cover classes; though the significant interaction between season and *L. cuneata* cover indicates their numbers varied inconsistently and this finding is reasonable, given the potentially cyclic nature of small mammal populations (Boonstra et al. 1998). Within the Great Plains, *P. leucopus*

is rarely found in habitats lacking woody plants (Kaufman et al. 1983; Schweiger et al. 2000), which were a component of each sample plot in quantities apparently sufficient to maintain this predominantly woodland species despite varying *L. cuneata* cover. The negative relationships between the bare ground variable and vegetation height variables for each species across tested *L. cuneata* cover classes is indicative of the importance of movement ease and quick escape from ground-based predators (e.g., *Lynx rufus*; Godbois et al. 2003) in areas with sufficient overhead concealment to provide protection from airborne predators (e.g., *Strix* spp.; Hedrick et al. 1989). This was likely true for the relatively large-bodied *S. hispidus*, which prefers dense overhead herbaceous cover for predator concealment and also as a food source (Bowne et al. 1999; Rehmeier et al. 2005).

Influence of invasive plants on small mammal community composition has also been reported in other systems. Litt and Steidl (2011) found invasive *Eragrostis lehmanniana* (Lehmann lovegrass) to exert predictable influence on small mammal functional groups. In their study, *Sigmodon* species also benefitted at higher levels of plant invasion, which corresponded with an overall increase in herbaceous biomass. Though vegetation biomass measurements were not a component of my study, biomass of invasive plant species, including *L. cuneata*, is typically greater than the native grasses it displaces (Smith and Knapp 2001; Allred et al. 2009). Given this, the increased numbers of *S. hispidus* in the high-cover plots and positive relationship between catch for this species and *L. cuneata* cover could have been due to an overall increase in vegetation biomass due to greater *L. cuneata* cover in these plots. For example, *S. hispidus* abundance can increase with increased monocot and dicot production (McMurry et al.



1994), while others have reported *S. hispidus* abundance to be positively related to dense herbaceous vegetation (Kaufman et al. 1990; Bowne et al. 1999).

*Lespedeza cuneata* patches may have provided refuge for *S. hispidus* and other small mammals because the plant's suppression of native graminoids likely modified fire characteristics such as intensity, rates of spread, and percolation. Camp Gruber is frequently burned and immediate as well as post-fire interactions can temporally alter small mammal community composition due to the induced changes in heterogeneity of habitat structure, which through succession creates conditions suitable to differing small mammal species at differing times (Fuhlendorf et al. 2010). Seasonal fire timing and subsequent effects on vegetation are also important. High intensity warm-season wildfires, for example, can exert negative influence on small mammal richness (Letnic et al. 2005; Ojeda 1989), while cool-season prescribed fires can exert positive influence on small mammal community structure (Masters 1993; Yarnell et al. 2007). Additionally, absence of large grazers at the site likely further modified interactions historically responsible for shaping the structure and function of grasslands within the region (Knapp et al. 1998).

Little is known about the palatability or consumption of *L. cuneata* (i.e., plant tissue or seeds) among small mammals, but the combination of higher catch and mean weights for *S. hispidus* suggests benefit to this species. High tannin content in *L. cuneata* results in poor palatability and is thought to discourage foraging, but much of what is known was gained from early studies with cattle (Wilkins et al. 1953; Hoveland et al. 1969). Goats (*Capra* spp.) however readily consume the plant and actually benefit from the high tannin loads, which suppress helminthic infections (Hart 2000; Min and Hart

2003). No studies to date have evaluated the potential for helminthic suppression in small mammals. *Sigmodon hispidus* may have benefited from the relatively high complete-protein content of *L. cuneata* despite tannin loads (Cameron and Eshelman 1996; Cummings et al. 2007) as evidenced by mean weights that were significantly higher in the high-cover *L. cuneata* plots. Regardless, higher mean body mass for *S. hispidus* in the high-cover *L. cuneata* cover classes likely translates to overall higher survival and fitness than *S. hispidus* with less mass in the lower cover *L. cuneata* plots (Millar and Hickling 1990; Schulte-Hostedde et al. 2001)

## **Conclusions**

*Lespedeza cuneata* invasion favored *S. hispidus* as evidenced by increased relative abundance and body mass in the high-cover *L. cuneata* plots. Additional research is needed to identify if this finding was the result of increased *L. cuneata* or simply due to invasion resulting in increased herbaceous biomass, which is preferred by this species. As reported elsewhere for other systems and other invasive plants, small mammal response to *L. cuneata* invasion for the most part followed species-specific habitat preferences and life history characteristics. As invasion progresses, small mammal communities will likely be dominated by increased numbers of a relatively few species. Given their variable populations characterized by rapid loss and turnover, decreased small mammal diversity may very well translate into impacts among dependent fauna and important ecological processes to a degree not previously seen.

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## Tables

Table 1. Average relative cover and standard deviation (SD) by vegetation functional group for the three *L. cuneata* cover classes sampled during the 2010-2011 small mammal survey (N = 243 for each mean). For comparison, *L. cuneata* cover is shown in italics immediately below the total mean legume cover.

		<i>L. cuneata</i> cover class <sup>1</sup>		
		Low	Mid	High
Vegetation cover <sup>2</sup>	GRAM	61.13(23.20)	47.86(24.15)	38.71(20.82)
	FORB	3.99(4.62)	3.39(9.32)	3.29(8.51)
	SHRUB	11.74(14.23)	8.93(13.25)	7.67(12.14)
	TREE	7.60(15.52)	10.70(16.88)	7.92(14.97)
	ASTER	11.87(13.84)	10.13(10.85)	11.65(11.26)
	LEGUME	3.63(6.99)	19.00(18.57)	30.76(23.02)
	<i>LECU</i>	<i>2.99(4.65)</i>	<i>16.53(17.85)</i>	<i>28.01(20.09)</i>

<sup>1</sup> Low = < 5%, Mid = 15 – 20%, High = > 25% mean cover per m<sup>2</sup>

<sup>2</sup> GRAM = mean graminoid cover; FORB = mean forb cover; SHRUB = mean shrub cover; TREE = mean tree canopy cover; ASTER = mean aster cover; LEGUME = mean legume cover; LECU = mean *L. cuneata* cover

Table 2. Small mammals captured at Camp Gruber from February 2010 to December 2011.

<b>Species</b>		
<b>Scientific name</b>	<b>Common name</b>	<b>Count</b>
<i>Blarina hylophaga</i>	Elliot's Short-Tailed Shrew	2
<i>Microtus pinetorum</i>	Woodland Vole	4
<i>Neotoma floridana</i>	Eastern Wood Rat	12
<i>Peromyscus attwateri</i>	Texas Mouse	17
<i>Peromyscus leucopus</i>	White Footed Mouse	434
<i>Peromyscus maniculatus</i>	Deer Mouse	338
<i>Reithrodontomys fulvescens</i>	Fulvous Harvest Mouse	136
<i>Reithrodontomys humulis</i>	Eastern Harvest Mouse	3
<i>Reithrodontomys montanus</i>	Plains Harvest Mouse	33
<i>Sigmodon hispidus</i>	Hispid Cotton Rat	419
		Total = 1398

Table 3. Mean small mammal species richness estimates and standard deviations (SD) within three *L. cuneata* cover classes<sup>1</sup> (N = 24 for each estimate). Means did not significantly differ between cover classes ( $F = 1.124$ ,  $df = 2$ ,  $P = 0.42$ ).

Cover class <sup>1</sup>	Season				Total means by class
	Spring	Summer	Fall	Winter	
Low	2.4 (1.2)	1.6 (1.0)	2.6 (1.6)	2.3 (1.0)	2.2
Mid	2.2 (1.1)	1.7 (0.9)	2.3 (1.1)	3.0 (0.9)	2.3
High	2.0 (0.8)	1.5 (0.7)	2.0 (0.9)	2.9 (1.0)	2.1

<sup>1</sup> Low = < 5%, Mid = 15 – 20%, High = > 25% mean *L. cuneata* cover per m<sup>2</sup>

Table 4. Mean small mammal diversity ( $H'$ ) values and standard deviations (SD) by *L. cuneata* cover class<sup>1</sup> (N = 3 for each index value). Similar mean values are denoted by shared uppercase letters (Tukey's HSD  $P > 0.05$ ).

Cover class <sup>1</sup>	Season				Total means by class
	Spring	Summer	Fall	Winter	
Low	1.38 (0.12)	0.85 (0.48)	1.20 (0.27)	1.43 (0.08)	1.21 <sup>A</sup>
Mid	1.53 (0.16)	1.25 (0.08)	1.27 (0.22)	1.47 (0.11)	1.38 <sup>A</sup>
High	1.08 (0.21)	0.78 (0.07)	0.78 (0.29)	1.33 (0.08)	0.99 <sup>B</sup>

<sup>1</sup> Low = < 5%, Mid = 15 – 20%, High = > 25% mean *L. cuneata* cover per m<sup>2</sup>

Table 5. Akaike's second-order information criterion (AICc) results for *S. hispidus* catch models ( $\Delta\text{AICc} \leq 7$ ).

Model parameters <sup>1</sup>										DF	AICc	$\Delta\text{AICc}$	$w_i$
INT	V1	V2	BG	LC	RG	GL	SE	VR	LC*SE				
13.75	-10.76	-15.94	9.38	0.58		0.92		-4.56		7	253.8	0.00	0.353
15.24	-11.96	-18.55	10.35	0.67				-3.47		6	256.8	2.95	0.081

<sup>1</sup> INT = intercept; V1 = percent of vegetation between 0.1 to 0.5-m high; V2 = vegetation between 0.5 to 1.0-m high; BG = mean occurrence of bare ground; LC = *L. cuneata* cover class (dummy coded); RG = mean occurrence of rock or gravel; GL = grass litter; SE = season (dummy coded); VR = total plot vegetation richness; LC\*SE = mean *L. cuneata* cover \* season



Table 6. Akaike's second-order information criterion (AICc) results for *P. leucopus* catch models ( $\Delta\text{AICc} \leq 7$ ).

Model parameters <sup>1</sup>										DF	AICc	$\Delta\text{AICc}$	$w_i$
INT	V1	V2	BG	LC	RG	GL	SE	VR	LC*SE				
14.74	-9.47	-18.91	8.83	-0.26	-30.95	-2.38	-0.19		0.15	9	335.2	0.00	0.50
14.79	-9.50	-18.95	8.85	-0.26	-31.00	-2.38	-0.17	-2.39	0.16	10	338.9	3.72	0.07

<sup>1</sup> INT = intercept; V1 = percent of vegetation between 0.1 to 0.5-m high; V2 = vegetation between 0.5 to 1.0-m high; BG = mean occurrence of bare ground; LC = *L. cuneata* cover class (dummy coded); RG = mean occurrence of rock or gravel; GL = grass litter; SE = season (dummy coded); VR = total plot vegetation richness; LC\*SE = mean *L. cuneata* cover \* season

Table 7. Akaike's second-order information criterion (AICc) results for *P. maniculatus* catch models ( $\Delta\text{AICc} \leq 7$ ).

Model parameters <sup>1</sup>										DF	AICc	$\Delta\text{AICc}$	$w_i$
INT	V1	V2	BG	LC	RG	GL	SE	VR	LC*SE				
23.98	-19.49	-29.68	13.50			-2.56	0.21			6	242.9	0.00	0.385
25.83	-20.75	-32.16	15.17		-18.95	-3.28	0.22			7	244.8	1.93	0.146

<sup>1</sup> INT = intercept; V1 = percent of vegetation between 0.1 to 0.5-m high; V2 = vegetation between 0.5 to 1.0-m high; BG = mean occurrence of bare ground; LC = *L. cuneata* cover class (dummy coded); RG = mean occurrence of rock or gravel; GL = grass litter; SE = season (dummy coded); VR = total plot vegetation richness; LC\*SE = mean *L. cuneata* cover \* season

Table 8. Results of AIC-based model averaging procedure for *S. hispidus* catch rates.

Models with a  $\Delta\text{AICc} \leq 7$  and free of pretending variables (Anderson 2008) were used to generate coefficient estimates.

<b>Parameter<sup>1</sup></b>	<b>Estimate</b>	<b>Std. Error</b>	<b>Z-score</b>	<b>P-value</b>
Intercept	14.50	3.72	3.70	< 0.001
V1	-11.36	3.20	-3.36	< 0.001
V2	-17.25	4.71	-3.39	< 0.001
BG	9.87	2.41	3.89	< 0.001
LC	0.63	0.09	6.36	< 0.001
GL	0.92	--	2.39	0.02
VR	-4.1	1.01	-3.49	< 0.001

<sup>1</sup> INT = intercept; V1 = percent of vegetation between 0.1 to 0.5-m high; V2 = vegetation between 0.5 to 1.0-m high; BG = mean occurrence of bare ground; LC = *L. cuneata* cover class (dummy coded); GL = grass litter; SE = season (dummy coded); VR = total plot vegetation richness

Table 9. Results of AIC-based model averaging procedure for *P. leucopus* catch rates. Models with a  $\Delta\text{AICc} \leq 7$  and free of pretending variables (Anderson 2008) were used to generate coefficient estimates.

Parameter <sup>1</sup>	Estimate	Std. Error	Z-score	P-value
Intercept	14.77	3.18	4.21	< 0.001
V1	-9.49	2.77	3.09	< 0.001
V2	-18.93	3.97	4.37	< 0.001
BG	8.84	2.44	3.20	0.002
LC	-0.26	-0.16	1.49	0.14
RG	-30.96	14.18	2.09	0.04
GL	-2.38	0.77	2.62	0.009
SE	-0.18	0.14	1.56	0.12
VR	-2.39	--	0.02	0.98
LC*SE	0.16	0.05	2.77	0.006

<sup>1</sup> INT = intercept; V1 = percent of vegetation between 0.1 to 0.5-m high; V2 = vegetation between 0.5 to 1.0-m high; BG = mean occurrence of bare ground; LC = *L. cuneata* cover class (dummy coded); RG = mean occurrence of rock or gravel; GL = grass litter; SE = season (dummy coded); VR = total plot vegetation richness; LC\*SE = mean *L. cuneata* cover \* season

Table 10. Results of AIC-based model averaging procedure for *P. maniculatus* catch rates. Models with a  $\Delta\text{AICc} \leq 7$  and free of pretending variables (Anderson 2008) were used to generate coefficient estimates.

<b>Parameter<sup>1</sup></b>	<b>Estimate</b>	<b>Std. Error</b>	<b>Z-score</b>	<b>P-value</b>
Intercept	24.91	3.59	6.78	< 0.001
V1	-20.12	3.19	6.14	< 0.001
V2	-30.92	4.23	7.08	< 0.001
BG	14.34	2.56	5.35	< 0.001
GL	-2.92	0.54	4.82	< 0.001
SE	0.22	0.05	3.93	< 0.001
RG	-18.95	--	1.07	0.28

<sup>1</sup> INT = intercept; V1 = percent of vegetation between 0.1 to 0.5-m high; V2 = vegetation between 0.5 to 1.0-m high; BG = mean occurrence of bare ground; GL = grass litter; SE = season (dummy coded); RG = mean occurrence of rock or gravel

Table 11. Relative importance of the eight predictor variables, plus the interaction term, for the species model sets. Results were determined using Akaike's second-order information criterion (AICc).

Species	Predictor Variable <sup>1</sup>								
	V1	V2	BG	LC	RG	GL	SE	VR	LC*SE
<i>S. hispidus</i>	1.00	1.00	1.00	1.00	0.20	1.00	0.16	1.00	0.00
<i>P. leucopus</i>	1.00	1.00	1.00	1.00	0.69	1.00	1.00	0.09	1.00
<i>P. maniculatus</i>	1.00	1.00	1.00	0.00	0.21	1.00	1.00	0.00	0.00

<sup>1</sup> INT = intercept; V1 = percent of vegetation between 0.1 to 0.5-m high; V2 = vegetation between 0.5 to 1.0-m high; BG = mean occurrence of bare ground; LC = *L. cuneata* cover class (dummy coded); RG = mean occurrence of rock or gravel; GL = grass litter; SE = season (dummy coded); VR = total plot vegetation richness; LC\*SE = mean *L. cuneata* cover \* season

Table 12. Mean weights (g), total captured, and standard deviation (N, SD) for *S. hispidus* trapped from three differing *L. cuneata* cover classes<sup>1</sup>. Similar mean weights are indicated by shared uppercase letters (Tukey's HSD  $P > 0.05$ ).

Cover class <sup>1</sup>	Season				Total means by class
	Spring	Summer	Fall	Winter	
Low	75.4 (28, 19.7)	70.9 (13, 37.8)	64.6 (8, 12.9)	84.7 (20, 20.0)	76.0 <sup>A</sup>
Mid	69.3 (19, 16.8)	82.9 (14, 10.1)	79.5 (19, 19.7)	86.1 (33, 20.5)	80.3 <sup>A</sup>
High	88.3 (75, 23.0)	114.6 (53, 28.1)	91.5 (70, 36.2)	106.7 (67, 33.7)	99.1 <sup>B</sup>

<sup>1</sup> Low = < 5%, Mid = 15 – 20%, High = > 25% mean cover per m<sup>2</sup>

Figures

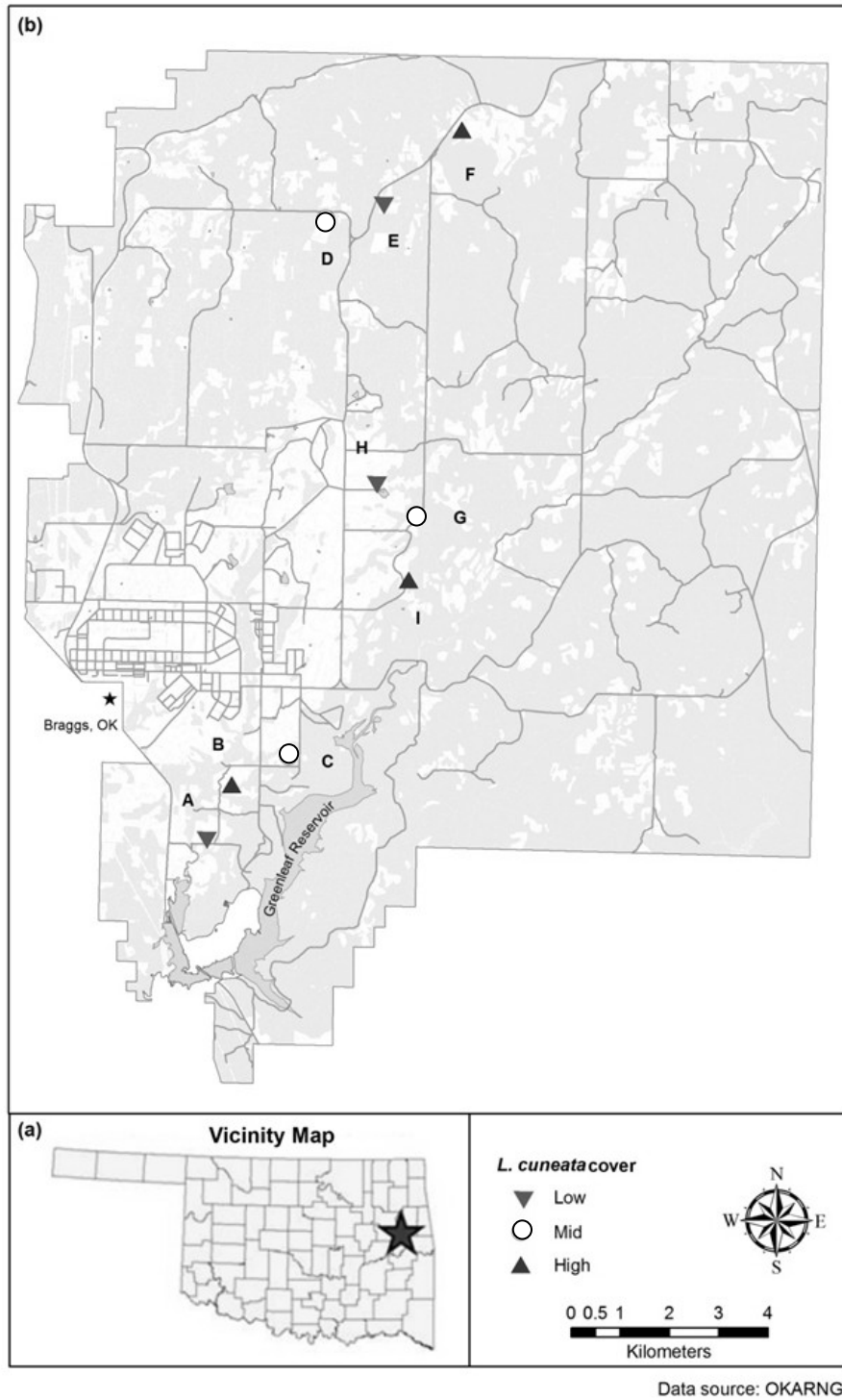


Figure 1. Map of Camp Gruber vicinity (a) and small mammal sampling plots (b).



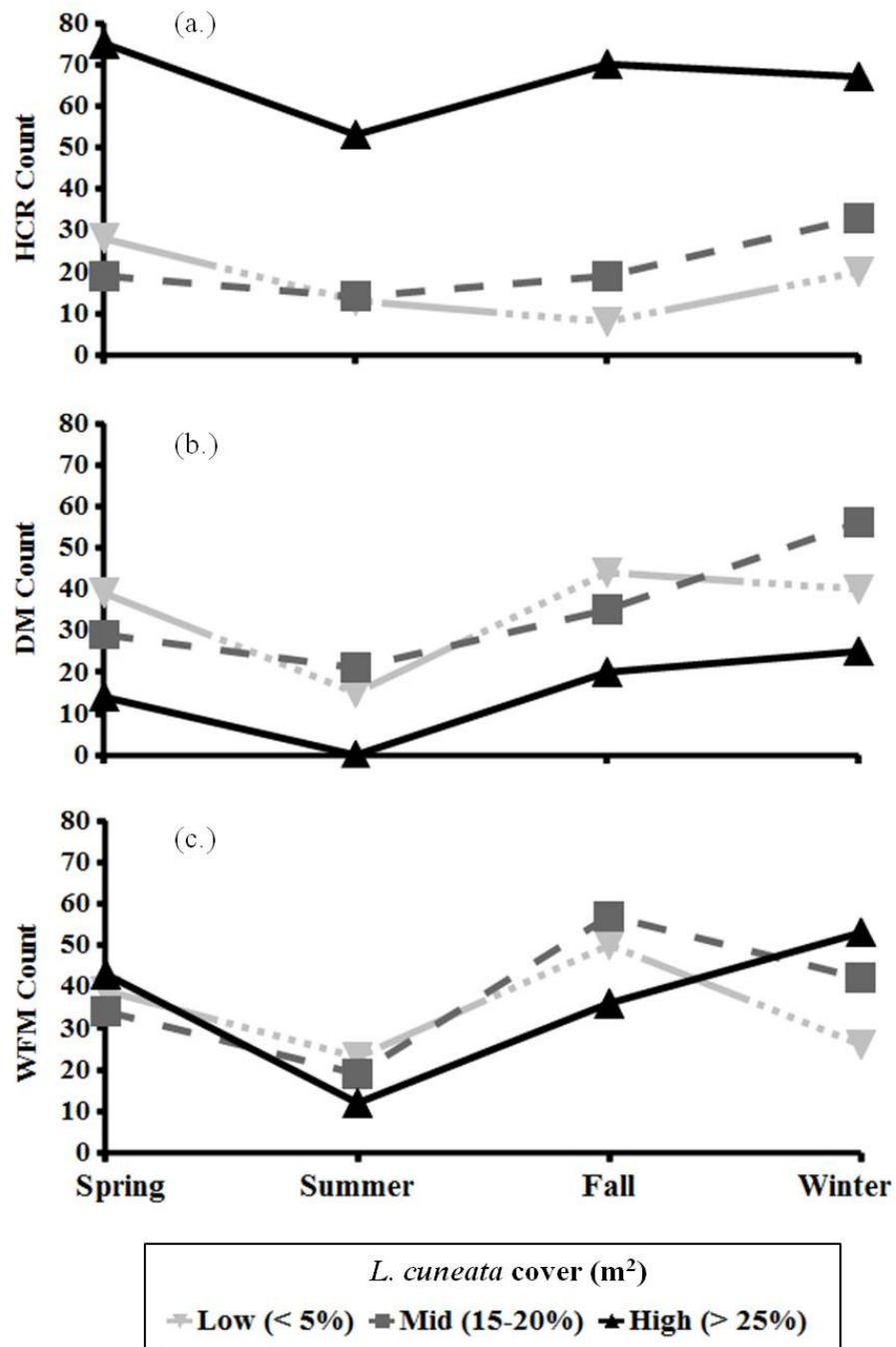


Figure 2. Total counts by season and *L. cuneata* cover for *S. hispidus* (HCR [hispid cotton rat]; a), *P. maniculatus* (DM [deer mouse]; b), and *P. leucopus* (WFM [white footed mouse]; c) trapped at Camp Gruber from February 2010 to December 2011.

APPENDIX A

Vegetation species recorded from the nine Camp Gruber sampling plots along with relative occurrence for each (percentage of the 729 total quadrats where present). For each plot, cover by species was estimated from 81 rigid 1-m<sup>2</sup> quadrats placed at 15-m intervals in a 9 x 9 grid arrangement.

Family	Scientific Name	Common Name	Acronym	Relative Presence (%)
<b>Trees</b>				
Cornaceae	<i>Cornus drummondii</i>	Rough-leaved dogwood	CODR	1.2
Ebenaceae	<i>Diospyros virginiana</i>	Persimmon	DIVI	12.6
Fabaceae	<i>Cercis Canadensis</i>	Redbud	CECA	0.3
	<i>Gleditsia triacanthos</i>	Honeylocust	GLTR	0.8
Fagaceae	<i>Quercus alba</i>	White oak	QUAL	0.1
	<i>Quercus marilandica</i>	Blackjack oak	QUMA	3.2
	<i>Quercus muehlenbergii</i>	Chinkapin oak	QUMU	1.4
	<i>Quercus stellata</i>	Post oak	QUST	5.2
Juglandaceae	<i>Carya alba</i>	Mockernut hickory	CAAL	0.1
	<i>Carya ovalis</i>	Pignut hickory	CAOV	0.3
Lauraceae	<i>Sassafras albidum</i>	Sassafras	SAAL	1.2
Oleaceae	<i>Fraxinus Americana</i>	White ash	FRAM	0.7
	<i>Fraxinus pennsylvanica</i>	Green ash	FRPE	0.5
Pinaceae	<i>Juniperus virginiana</i>	Eastern red cedar	JUVI	0.1
Rhamnaceae	<i>Rhamnus caroliniana</i>	Buckthorn	FRCA	0.1
Rosaceae	<i>Prunus serotina</i>	Black cherry	PRSE	0.1
Salicaceae	<i>Salix nigra</i>	Black willow	SANI	0.0
Sapotaceae	<i>Bumelia lanuginose</i>	Chittamwood	BULA	0.5
Ulmaceae	<i>Celtis laevigata</i>	Sugarberry	CELA	0.4
	<i>Celtis occidentalis</i>	Hackberry	CEOC	1.2
	<i>Ulmus alata</i>	Winged elm	ULAL	23.9
	<i>Ulmus Americana</i>	American elm	ULAM	0.1
	<i>Ulmus rubra</i>	Slippery elm	ULRU	0.1
<b>Woody Shrubs and Vines</b>				
Anacardiaceae	<i>Rhus aromatic</i>	Fragrant sumac	RHAR	0.7
	<i>Rhus copallina</i>	Winged sumac	RHCO	25.9
	<i>Toxicodendron radicans</i>	Poison Ivy	TORA	0.5
Bignoniaceae	<i>Campsis radicans</i>	Trumpet vine	CARA	0.5

Family	Scientific Name	Common Name	Acronym	Relative Presence (%)
Caprifoliaceae	<i>Symphoricarpos orbiculatus</i>	Coralberry	SYOR	9.5
Convolvulaceae	<i>Calystegia sepium</i>	Hedge false bindweed	CASE	0.1
Ericaceae	<i>Vaccinium stamineum</i>	Deerberry	VAST	0.1
Passifloraceae	<i>Passiflora incarnate</i>	Purple passionflower	PAIN	3.8
Rosaceae	<i>Crataegus crus-galli</i>	Cockspur hawthorn	CRCR	0.7
	<i>Crataegus sp.</i>	Hawthorn	CRTG-SP	0.1
	<i>Prunus Americana</i>	American plum	PRAM	1.2
	<i>Prunus Mexicana</i>	Mexican plum	PRME	0.4
	<i>Rubus aboriginum</i>	Northern dewberry	RUAB	8.2
	<i>Rubus sp.</i>	Blackberry	RUBS	7.8
	<i>Rosa setigera</i>	Climbing rose	ROSE	0.3
	<i>Rosa multiflora</i>	Multiflora rose	ROMU	0.1
Sapindaceae	<i>Sapindus saponaria</i>	Soapberry	SASA	1.5
Vitaceae	<i>Parthenocissus quinquefolia</i>	Virginia Creeper	PAQU	0.4
<b>Dicotyledons (Forbs / Herbaceous Plants)</b>				
Acanthaceae	<i>Ruellia humilis</i>	Low ruellia	RUHU	0.5
Apocynaceae	<i>Apocynum cannabinum</i>	Indianhemp	APCA	0.5
Asclepiadaceae	<i>Asclepias viridis</i>	Spider milkweed	ASVI	0.5
Asteraceae	<i>Achillea millefolium</i>	Common yarrow	ACMI	11.7
	<i>Ambrosia artemisiifolia</i>	Common ragweed	AMAR	3.4
	<i>Ambrosia bidentata</i>	Lanceleaf ragweed	AMBI	3.6
	<i>Ambrosia psilostachya</i>	Cuman ragweed	AMPS	1.4
	<i>Amphiachyris dracunculoides</i>	Common broomweed	AMDR	0.1
	<i>Arnoglossum plantagineum</i>	Indian plantain	ARPL	0.3
	<i>Artemisia biennis</i>	White sagebrush	ARBI	1.5
	<i>Boltonia asteroides</i>	False starwort	BOAS	0.3
	<i>Brickellia eupatorioides</i>	False boneset	BREU	1.6
	<i>Centaurea Americana</i>	American basketflower	CEAM2	0.4
	<i>Cirsium altissimum</i>	Tall thistle	CIAL	1.5
	<i>Coreopsis tinctoria</i>	Plains coreopsis	COTI	0.4
	<i>Eryngium yuccifolium</i>	Button eryngo	ERYU	0.4
	<i>Eupatorium serotinum</i>	Late boneset	EUSE	0.1
	<i>Euthamia graminifolia</i>	Flat-top goldenrod	EUGR	14.7
<i>Helianthus x laetiflorus</i>	Cheerful sunflower	HELA	0.7	
<i>Iva angustifolia</i>	Narrowleaf ragweed	IVAN	0.8	

Family	Scientific Name	Common Name	Acronym	Relative Presence (%)
Asteraceae	<i>Liatriis aspera</i>	Tall gayfeather	LIAS	2.6
	<i>Liatriis pycnostachya</i>	Button snakeroot	LIPY	1.0
	<i>Ratibida columnifera</i>	Yellow coneflower	RACO	0.1
	<i>Rudbeckia hirta</i>	Blackeyed Susan	RUHI	2.5
	<i>Solidago arguta</i>	Goldenrod	SOAR	0.3
	<i>Solidago Canadensis</i>	Canada goldenrod	SOCA	13.4
	<i>Solidago missouriensis</i>	Missouri goldenrod	SOMI	0.8
	<i>Solidago gigantean</i>	Giant goldenrod	SOGI	1.1
	<i>Solidago nemoralis</i>	Old field goldenrod	SONE	1.8
	<i>Solidago radula</i>	Goldenrod	SORA	0.1
	<i>Solidago rugosa</i>	Rough-leaved goldenrod	SORU	1.4
	<i>Symphyotrichum ericoides</i>	White heath aster	SYER	8.2
	<i>Symphyotrichum patens</i>	Late purple aster	SYPA	8.2
	<i>Symphyotrichum praealtum</i>	Willowleaf aster	SYPR	5.6
	<i>Symphyotrichum sp.</i>	Aster	SYM-SP	1.0
	<i>Verbesina helianthoides</i>	Crownbeard	VEHE	0.4
	<i>Verbesina virginica</i>	Whitewind	VEVI	3.4
<i>Vernonia baldwinii</i>	Western ironweed	VEBA	0.8	
Cactaceae	<i>Opuntia macrorhiza</i>	Twistspine pricklypear	OPMA	0.3
Campanulaceae	<i>Triodanis perfoliata</i>	Venus' looking-glass	TRPE	0.0
Euphobiaceae	<i>Acalypha gracilens</i>	Three-seeded mercury	ACGR	0.7
	<i>Acalypha virginica</i>	Three-seeded mercury	ACVI	0.1
	<i>Croton capitatus</i>	Woolly croton	CRCA	1.4
	<i>Croton monanthogynus</i>	One-seeded croton	CRMO	6.9
	<i>Croton willdenowii</i>	Willdenow's croton	CRWI	1.1
	<i>Tragia betonicifolia</i>	Nettleleaf	TRBE	0.1
Fabaceae	<i>Acacia angustissima</i>	Prairie acacia	ACAN	1.2
	<i>Amorpha canescens</i>	Leadplant	AMCA	0.4
	<i>Amorpha fruticosa</i>	False indigo	AMFR	0.0
	<i>Baptisia bracteata</i>	Plains wild indigo	BABR	0.3
	<i>Baptisia alba</i>	Plains wild indigo	BAAL	0.3
	<i>Clitoria mariana</i>	Atlantic pigeonwings	CLMA	0.3
	<i>Desmodium glabellum</i>	Panicled tickclover	DEGL	1.0
	<i>Desmodium paniculatum</i>	Panicled leaf ticktrefoil	DEPA	1.6
	<i>Desmodium sessilifolium</i>	Sessile tickclover	DESE	0.5
	<i>Lespedeza capitata</i>	Bush clover	LECA	1.0

Family	Scientific Name	Common Name	Acronym	Relative Presence (%)
Fabaceae	<i>Lespedeza cuneata</i>	Sericea lespedeza	LECU	54.6
	<i>Lespedeza hirta</i>	Hairy lespedeza	LEHI	0.1
	<i>Lespedeza procumbens</i>	Trailing lespedeza	LEPR	3.8
	<i>Lespedeza repens</i>	Creeping lespedeza	LERE	0.4
	<i>Lespedeza stuevei</i>	Stuve's lespedeza	LEST	0.8
	<i>Lespedeza violacea</i>	Violet lespedeza	LEVI2	3.2
	<i>Lespedeza virginica</i>	Slender lespedeza	LEVI	6.2
	<i>Mimosa nuttallii</i>	Nuttall's sensitive-briar	MINU	1.8
	<i>Neptunia lutea</i>	Yellow puff	NELU	0.1
Lamiaceae	<i>Monarda fistulosa</i>	Wild bergamot	MOFI	0.8
	<i>Pycnanthemum tenuifolium</i>	Narrowleaf mountainmint	PYTE	6.7
	<i>Teucrium canadense</i>	American germander	TECA	3.8
Oxalidaceae	<i>Oxalis corniculata</i>	Yellow wood sorrel	OXCO	0.3
	<i>Oxalis violacea</i>	Violet wood sorrel	OXVI	0.1
Polygonaceae	<i>Rumex acetosella</i>	Common sheep sorrel	RUAC	0.1
Rubiaceae	<i>Diodia teres</i>	Rough buttonweed	DITE	0.4
Scrophulariaceae	<i>Agalinis fasciculata</i>	Beach agalinis	AGFA	0.1
Solanaceae	<i>Physalis heterophylla</i>	Clammy ground cherry	PHHE	0.1
	<i>Physalis pumila</i>	Dwarf ground cherry	PHPU	0.3
	<i>Solanum carolinense</i>	Carolina horsenettle	SOCA2	2.3
	-	Unknown forb	UNK-F	0.7
<b>Monocotyledons ( Grasses, Sedges, Lilies, etc.)</b>				
Cyperaceae	<i>Carex sp.</i>	Sedge	CARX	27.7
	<i>Cyperus acuminatus</i>	Taperleaf flatsedge	CYAC	0.7
	<i>Cyperus sp.</i>	Sedge	CYPR	0.3
Juncaceae	<i>Juncus acuminatus</i>	Jointed rush	JUAC	0.3
	<i>Juncus tenuis</i>	Slender rush	JUTE	3.3
	<i>Juncus sp.</i>	Rush	JUNC-SP	0.1
Orchidaceae	<i>Spiranthes lacera</i>	Northern slender ladies' tresses	SPLA	8.1
Poaceae	<i>Andropogon gerardii</i>	Big bluestem	ANGE	7.0
	<i>Andropogon ternaries</i>	Splitbeard bluestem	ANTE	2.9
	<i>Andropogon virginicus</i>	Broomsedge bluestem	ANVI	1.0
	<i>Aristida longespica</i>	Slimspike threeawn	ARLO	1.5
	<i>Aristida purpurascens</i>	Arrowfeather threeawn	ARPU	2.5
	<i>Bromus japonicas</i>	Japanese bromegrass	BRJA	11.9

Family	Scientific Name	Common Name	Acronym	Relative Presence (%)
Poaceae	<i>Chasmanthium latifolium</i>	Inland sea oats	CHLA	11.8
	<i>Coelorachis cylindrica</i>	Carolina jointgrass	COCY	0.7
	<i>Dichantherium boscii</i>	Bosc panicum	DIBO	1.4
	<i>Dichantherium linearifolium</i>	Slimleaf panicum	DILI	6.2
	<i>Dichantherium oligosanthes</i>	Heller's rosette grass	DIOL	44.3
	<i>Digitaria cognate</i>	Fall witchgrass	DICO	2.3
	<i>Elymus Canadensis</i>	Canada wildrye	ELCA	6.9
	<i>Elymus virginicus</i>	Virginina wild rye	ELVI	8.9
	<i>Eragrostis spectabilis</i>	Purple lovegrass	ERSP	7.5
	<i>Eragrostis trichodes</i>	Sand lovegrass	ERTR	0.5
	<i>Muhlenbergia sobolifera</i>	Rocky muhly	MUSO	3.6
	<i>Gymnopogon ambiguus</i>	Bearded skeletongrass	GYAM	6.6
	<i>Panicum anceps</i>	Beaked panicum	PAAN	8.6
	<i>Panicum virgatum</i>	Fall switchgrass	PAVI	5.6
	<i>Paspalum floridanum</i>	Florida paspalum	PAFL	0.8
	<i>Poa annua</i>	Annual bluegrass	POAN	1.2
	<i>Schedonorus phoenix</i>	Tall fescue	SCPH	0.1
	<i>Schizachyrium scoparium</i>	Little bluestem	SCSC	51.2
	<i>Setaria pumila</i>	Yellow foxtail	SEPU	7.7
	<i>Sorghastrum nutans</i>	Indiangrass	SONU	6.6
	<i>Sporobolus asper</i>	Meadow dropseed	SPAS	1.5
	<i>Sporobolus clandestinus</i>	Meadow dropseed	SPCL	1.2
	<i>Tridens flavus</i>	Purpletop	TRFL	11.9
	<i>Tridens strictus</i>	Lonspike tridens	TRST	2.5
	<i>Vulpia octoflora</i>	Six weeks fescue	VUOC	0.1
	-	Unknown grass	UNK-G	1.2

APPENDIX B

Relative canopy heights by plot and *Lespedeza cuneata* cover class (as % of total). Data were recorded at 0.5 intervals along four 4 x 135-m belt transects (N = 544).

		Plot								
		A	B	C	D	E	F	G	H	I
		Low	High	Mid	Mid	Low	High	Mid	Low	High
Vertical Canopy Height (m)	<i>L. cuneata</i> cover class <sup>1</sup>									
	< 0.5	0.78	0.85	0.65	0.64	0.69	0.41	0.52	0.85	0.65
	0.51-1.0	0.11	0.13	0.16	0.11	0.11	0.12	0.13	0.13	0.16
	1.1-1.5	0.03	0.02	0.04	0.03	0.06	0.03	0.01	0.01	0.04
	1.6-2.0	0.02	0.01	0.00	0.02	0.02	0.04	0.00	0.00	0.00
	2.1-2.5	0.00	0.00	0.00	0.01	0.01	0.02	0.01	0.00	0.00
	2.6-3.0	0.00	0.00	0.00	0.01	0.01	0.02	0.01	0.00	0.00
	3.1-3.5	0.00	0.00	0.00	0.02	0.01	0.02	0.01	0.00	0.00
	3.6-4.0	0.01	0.00	0.00	0.02	0.01	0.02	0.02	0.00	0.00
	4.1-4.5	0.00	0.00	0.00	0.02	0.01	0.03	0.02	0.00	0.00
	4.6-5.0	0.01	0.00	0.00	0.02	0.01	0.02	0.02	0.00	0.00
	5.1-5.5	0.00	0.00	0.00	0.02	0.01	0.03	0.02	0.00	0.00
	5.6-6.0	0.00	0.00	0.00	0.02	0.01	0.03	0.02	0.00	0.00
	6.1-6.5	0.00	0.00	0.00	0.01	0.01	0.03	0.02	0.00	0.00
	6.6-7.0	0.01	0.00	0.00	0.02	0.00	0.03	0.03	0.00	0.00
	7.1-7.5	0.00	0.00	0.00	0.01	0.00	0.03	0.03	0.00	0.00
7.6-8.0	0.00	0.00	0.00	0.01	0.00	0.03	0.03	0.00	0.00	
8.1-8.5	0.00	0.00	0.00	0.01	0.00	0.03	0.03	0.00	0.00	

<sup>1</sup> Low = < 5%, Mid = 15 – 20%, High = > 25% mean cover per m<sup>2</sup>

## CHAPTER III

### THE INFLUENCE OF LOCAL FIRE HISTORY ON *LESPEDEZA CUNEATA* INVASION

#### **Abstract**

*Lespedeza cuneata* is an invasive perennial legume first introduced to North America from Asia in 1896. The plant is now well established across much of the eastern and central United States in a variety of habitats. Mechanisms of spread however are poorly understood, but evidence suggests a positive fire response. The purpose of my investigation was to examine the relationship between fire history and *L. cuneata* cover, as well as the relationships between *L. cuneata* cover and the vegetation community. For this, I constructed local fire histories using sectioned *Quercus stellata* trees and also collected detailed vegetation community data within these same areas. Mean fire return interval (MFI) alone explained 75% of the variation in *L. cuneata* cover and the relationship was negative. Additionally, I detected a negative relationship between *L. cuneata* invasion and graminoid cover. My findings describe for the first time a relationship between MFI and *L. cuneata* cover and I provide evidence of how invasive plant species are capable of influencing important ecological conditions under which native species evolved.



## **Introduction**

Habitat management and restoration involves establishing clear goals and supporting objectives, with the underlying assumption that actions will favorably move the system closer to the desired outcome. However, when those endpoints are modeled on historical communities (e.g., Swetnam et al. 1999), confounding results can occur as ecosystems are dynamic and rarely static. Reintroduction of processes following an exclusion period may allow sufficient time for divergence or modification during the hiatus. For example, huge numbers of invasive species have been introduced to North America since European colonization, with approximations approaching 50,000 taxa (Westbrooks 2004) and while many have failed to establish, some of the species that have established are capable of modifying the structure and composition of native communities (e.g., Fleishman et al. 2003). Additionally, climatic conditions are rapidly changing and alter the characteristics and influence of important disturbance regimes, such as fire timing, frequency, and severity (Turner 2010).

Fire suppression was well established in governing policy from the late 1800s to the mid 1940s, when the first prescribed fire use on federal lands was permitted in the United States (Bickford and Newcomb 1946) and not until the late 1960s were western forests treated with prescribed fire (Stephens and Ruth 2005). Introduction elsewhere on both state- and federally managed lands has been slow, but persistent. From 1960 to 2003, prescribed fire use in the United States increased dramatically, with over 2.2 million ha burned in 2003 (Stephens and Ruth 2005). However, modified climatic conditions, disturbance regimes and species introductions have created new and novel

assemblages that may differ greatly from those that existed prior to fire exclusion (Harris et al. 2006; Jackson and Hobbs 2009).

*Lespedeza cuneata* is a perennial invasive legume first introduced to North America from Asia in 1896 (Davison 1941). Initial plantings were limited until the 1930s when perceived wildlife benefit and use for erosion control increased popularity among state and federal agencies (Eddy and Moore 1998). Additional introductions occurred due to the plant's ability to establish and grow in poor and disturbed soils (Ohlenbusch et al. 2007). Prolific seed production and allelopathic properties helped quickly establish *L. cuneata* in a wide range of habitats from the eastern to the central United States, especially within disturbed native prairies and rangelands (Kalburtji et al. 2001; Cummings et al. 2007b).

Few studies have evaluated potential relationships between fire return interval and *L. cuneata* despite evidence to suggest a possible relationship. Fire has a neutral to positive effect on *L. cuneata* once the plant is established, which is facilitated by *L. cuneata*'s ability to re-sprout following top kill and enhanced germination rates via scarification and seed bank exposure (Wong 2012). Many of these fire tolerant qualities are shared with native fire-adapted plant species; however, couple these fire tolerant traits with *L. cuneata*'s high seed production, rapid growth, allelopathy, shading, and detrital deposition and the means necessary to facilitate ecosystem alteration through multiple pathways becomes more apparent. Additionally, the capability to establish dense, monoculture stands suggests *L. cuneata* can displace native plants, but few have evaluated this among different *L. cuneata* cover classes. For these reasons my objective was to 1) use dendrochronological data to examine the relationships between *L. cuneata*

cover and mean fire return interval, fire frequency, and the average number of fires per decade and to 2) evaluate the impact of *L. cuneata* invasion on plant functional groups.

## **Methods**

*Study site* - The 13,366-ha Camp Gruber Training Center (CGTC) is located in northeastern Muskogee County, Oklahoma and is bordered to the north and west by rural agricultural areas. On the eastern boundary, the training center adjoins the 12,502-ha Cherokee Wildlife Management Area (CWMA) and the two areas are known collectively as “Camp Gruber” (Figure 1). About 64% (8,553-ha) of CGTC and 86% (10,752-ha) of the CWMA consist of woody vegetation, while the remainder of both are grasslands or savannas (4,812-ha and 1,750-ha, respectively), as determined from digitization of color aerial photography collected in 2011 and previous reports by Woolf and Miller (2009).

Agriculture was the most prevalent use of the site from settlement until the United States government acquisition began in 1935. Between 1936 and 1942, the United States Department of Agriculture enacted the Eastern Oklahoma Cookson Hills Forestry, Fish, and Game Project, which turned much of present day CGTC into a wildlife management and recreation area. A military acquisition program also began during this time and by 1942 added more than 14,973-ha, resulting in a total of 26,279-ha (U.S. Forest Service 1977). Camp Gruber opened on 12 May 1942 and served as a primary infantry and support group training base for the U.S. Army until deactivation on 3 June 1947. Military use of the Muskogee County portion resumed when the Oklahoma Army National Guard took control of the site in 1977. Though the site has been used for military training, other

anthropogenic influences such as agriculture and urbanization have been excluded since 1935.

Exact timing for *L. cuneata* arrival at CGTC is unknown; however, Little (1938) did not report *L. cuneata* among the 829 species recorded for the region in an early survey. Introduction likely occurred afterwards during the 1940s Cookson Hills Project. By 1992 the plant was noted as present in flora surveys conducted by Johnson et al. (1994) and later estimated to be well established on at least 120-ha in 1996 (Schnell et al. 1997). Remote sensing imagery (low-level color infrared) collected during the fall of 2006 indicated *L. cuneata* invasion had progressed to detectable levels on 1,363-ha (4-ha minimum map unit).

Since military use began at CGTC training activities have sparked numerous wildfires (Howard 2011). Prescribed fire use at the site has also been frequent and used for ecological management and to reduce fuel loads. The current prescription goal (initiated in 2003) is treatment of one-third of CGTC (approximately 4,000-ha) annually on a three year rotation, with most fires planned during the dormant season (Howard 2011).

*Fire history assessment* – I collected 110 total *Quercus stellata* cross sections from the nine plot locations during summer 2012 for the fire history assessment (Figure 1). All specimens were obtained from live trees situated in locations that ranged in slope from generally flat (0-1 % slope) to slightly steeper (10-15 % slope), while orientation aspects were variable. In addition to being common across the study site, I chose *Q. stellata* trees for the analysis because they are sensitive to fire scarring, establish readily identifiable annual growth rings, and have been successfully used by other researchers for

reconstructing historical fire regimes within the region (DeSantis et al. 2010; Allen and Palmer 2011; Fan et al. 2012).

I sampled trees following a stratified-random approach near nine plots, each situated in one of three mean *L. cuneata* cover classes (i.e., low [0 – 5% coverage/m<sup>2</sup>], mid [15 – 20% coverage/m<sup>2</sup>], and high [ $> 25\%$  coverage/m<sup>2</sup>]) (Woolf and Miller 2009). Specifically, for each of the nine plots I used the data management tools in ArcGIS to delineate a circular perimeter (0.5 km radius) around plot center points and divided this area further into equal-area quarter sections. I then generated 12 points for each whole perimeter, with allocation in each quarter based on the relative tree cover determined from 2011 leaf-on aerial imagery. For example, if one quarter contained 50% of the trees, then 6 points were allocated there. A hand-held GPS loaded with the generated points was used afield to locate the nearest *Q. stellata* specimens to each generated point. Relatively wide distribution of *Q. stellata* allowed location of at least three specimen trees within each quadrant quarter for eight of the nine plots (see Appendix). However for plot H the northeast and northwest quarters lacked *Q. stellata* trees and for this reason, 6 trees were sampled in each of the other 2 quarters.

Fire histories were known to vary among the nine plot locations and this was influential on plot selection, as was varying *L. cuneata* cover; however, the exact degree of fire history variation prior to about 1990 was unknown at the time of plot selection (Howard 2011). Other factors influential to plot selection included ease of accessibility, similarity of topology and terrain (compared using 1:24,000 USGS topographic maps), as well as caveats unique to an active military training site (e.g., avoidance of firing range surface danger zones and areas containing unexploded ordinance).

All cross sections were cut from live trees within 30-cm of the ground surface and the north side of all trunks was uniquely marked (with paint) to facilitate later identification. Field-recorded parameters included trunk diameter 10-cm above ground level, diameter at breast height (1.4-m; DBH), geographic coordinates, aspect, slope and elevation. Collected cross sections were surfaced using electric sanders with successively finer grit sandpaper (i.e., 36, 80, 120, 220, 400, 800, 1000 and 1200 grit). Calendar years for each section were determined by cross-dating tree rings using skeleton plots (Stokes and Smiley 1968). Ring widths were then determined using a dissecting scope and calibrated Velmex stage. Subsequent to tree ring analysis skeleton plots for these specimens were evaluated against the regional master chronology.

I used the program MeasureJ2X to collect and organize output from the Velmex system and validated the accuracy of measurements using the COFECHA program (Holmes 1983). Fire scars were visually identified following recommendations by Smith and Sutherland (2001). That is, fire scars were determined using a combination of diagnostics, which included presence of elongated or triangular scars, cambial injury and callus, charcoal presence, and highly variable ring widths. Detected scars were assigned to the first year of growth response present in the wound, while seasonality (i.e., dormant, earlywood, latewood, or undetermined) was assigned by evaluating scar position within the ring. I used the FXH2 program to calculate the mean fire return interval (MFI) separately for each of the nine permanent plots (Grissino-Mayer 2001) and modeled MFI using the Weibull distribution (due to lack of data normality).

*Vegetation sampling* – I collected detailed vegetation community data at the nine permanent plots from 12-21 September 2011 using 1-m<sup>2</sup> rigid quadrats

(polyvinylchloride construction) placed at 15-m intervals along a 9 x 9 grid pattern (135 x 135-m). I arranged quadrats in a north-south orientation and the plot served as center for the 0.5-km buffer used to define the *Q. stellata* collection bounds. Relative species cover was estimated for each quadrat. I also surveyed four randomly selected 4-m wide by 135-m long linear transects in a north-south orientation vegetation community grid (135 x 135-m) to describe ground cover for each of the nine sample plots. This was done by lowering a 1.0-cm rod vertically to one side of the transect at 0.5-m intervals and categorizing intersected ground conditions.

*Statistical analysis* – I examined variation in the mean number of fires per decade within each of the three *L. cuneata* cover classes using separate rm-ANOVAs and followed significant findings with Tukey’s HSD to identify differing means. For the vegetation data, I used regression models to examine the influence of relevant predictor variables (i.e., MFI, years since last fire, number of fires since 2000 to 2010) on arcsine transformed vegetation cover data (i.e., mean *L. cuneata*, graminoid, shrub, and forb percent cover). Additionally, I used correlation analysis to identify relationships between mean *L. cuneata* cover and vegetation and ground cover data, which were summarized from the four belt transects surveyed at each of the 9 plots (as opposed to summary by the plot as a whole) to increase degrees of freedom.

## **Results**

*Fire history assessment* – I identified 160 total fire scars from the *Q. stellata* cross sections (Figure 2). Ninety-two percent of identified scars were in the dormant season (92%), while seasonality for 5% went undetermined. The remaining 2% and 1% of the

fire scars were associated with earlywood (early growing season) and latewood (late growing season), respectively. Mean fire return interval (MFI) ranged from 1.8 to 7.1 years (Table 1) and the overall MFI (all specimens pooled) for the study area was 4.1 years (SD = 1.7). Individual plot MFI provided insight into underlying relationships between local fire histories and the vegetation community. This variation in plot MFI was possible in relatively small spatial areas due to the well-established trail network that functions to compartmentalize both prescribed and wildfires (personal communication, Camp Gruber Wildland Fire Manager).

I collected an adequate amount of dendrological data to compare mean fires per decade among *L. cuneata* cover classes from the 1960s onward and found fires to temporally increase in all cover classes (Figure 3). However, differences were only significant for the high cover plots ( $F = 5.659$ ,  $df = 4$ ,  $P = 0.02$ ) where the mean number of fires increased fifteen-fold from the 1960s to 2000s. Post hoc comparison indicated the higher mean number of fires in the 2000s (mean = 5.0, SD = 1.0) to significantly differ from the 1960s and 1970s means (mean = 0.33, SD = 0.6 for both), but the number of fires in the 2000s did not significantly differ the 1980s and 1990s means (2.3, SD = 2.5 and 3.0, SD = 2.0, respectively).

Simple regression with mean fire return interval as a single predictor best explained variation in mean *L. cuneata*, graminoid, and shrub cover. Both the time since last fire and number of fires from 2000 to 2010 variables were insignificant predictors. Mean fire return interval explained 75% of the variation in mean *L. cuneata* cover and the overall highest *L. cuneata* cover occurred in the most frequent fire areas (Figure 4). Mean coverage ranged from 31% at a MFI of 1.8 years, to near 0% for plots at the upper



end of the observed MFI range (> 5 years). I detected a positive relationship between graminoid cover and MFI (75% of the variation explained; Figure 5a). Mean fire return interval explained 88% of observed variation in shrub cover and the relationship was positive (Figure 5b); however, MFI explained little variation in relative forb cover (Figure 5c). Time since last fire and number of fires from 2000 to 2010 were insignificant predictors of forb cover.

*Vegetation sampling* – I identified 157 plant species during the vegetation surveys (see Chapter 2 Appendix A). Families represented by the most taxa included the Asteraceae (N = 35), Poaceae (N = 32), and Fabaceae (N = 19). Forbs (herbaceous dicots) were most common with 77 taxa, followed by grasses/sedges and other monocots with 39 taxa. Trees and woody vines/shrubs were represented by 23 and 18 taxa, respectively. Plot A supported the greatest plant species richness with 68 taxa recorded (quadrat mean = 8.0, SD = 2.3), while plot I contained the fewest species at 42 taxa (quadrat mean = 4.8, SD = 1.5; Table 1). Interestingly, the plot A MFI was one of the longest observed (6 years), while the shortest MFI occurred at plot I (1.8 years); however, relationships between MFI and vegetation among the other plots were more variable (Table 1).

Results of the correlation analysis indicated relationships between vegetation and ground cover and mean *L. cuneata* cover were consistent for parameters across *L. cuneata* cover classes (Table 2). Differing however was the strength of relationships, which were mostly significant for the high-cover *L. cuneata* plots, with the exception of the slight negative relationships between mean *L. cuneata* cover and total plot vegetation richness and rock/gravel ground cover. Within the high-cover *L. cuneata* plots, a positive

relationship occurred between mean *L. cuneata* cover and bare ground, while relationships between mean *L. cuneata* and mean grass litter, graminoid cover, shrub cover, and fire return interval were each negative. For the other two cover classes, only the negative relationship between mean *L. cuneata* and the mid-cover mean fire return interval was significant.

## **Discussion**

The progressive invasion of woody plants into grassland ecosystems is well documented (e.g., Briggs et al. 2005; Brook and Bowman 2006). Even under highly variable fire regimes the persistence and expansion of shrub cover within grasslands has been demonstrated (Heisler et al. 2003). Cited reasons are many, but encroachment due to fire suppression is common (Knapp et al. 1998; Archer et al. 2001; Briggs and Knapp 2001; Hoch et al 2002) along with alteration of fine fuel loads and resulting fire intensity modification (Scholes and Archer 1997). My results align well with these previous findings by showing a strong positive relationship between increased shrub cover and longer fire intervals. Additionally, I found varying fire return intervals to have little impact on forbs, which agrees with findings by Abrams and Hulbert (1987). Differing among published reports however is my finding that graminoid cover also increased positively with the mean fire return interval. Others have shown the grassland-woody plant balance to be inversely linked, with advancement of one functional group typically coming at the expense of the other (Axelrod 1985). My inclusion of *L. cuneata* offers a possible explanation of this unique and seemingly counterintuitive finding.

Similar negative relationships between *L. cuneata* invasion and native grass biomass have been reported in managed rangeland (Cummings et al. 2007a), as well as for non-grazed areas of moderate to heavy *L. cuneata* invasion (12-40 plants/m<sup>2</sup>) (Farris 2006). Few others have reported the apparent negative relationship between *L. cuneata* and graminoid species and additional research is needed to identify how invasion and subsequent graminoid suppression may alter local fire characteristics (e.g., fire intensity and severity, spread, percolation, etc.). The majority of fires I recorded (92%) occurred during the dormant season. Historically within the region fires occurred throughout the year in a variety of differing climatic conditions (Knapp et al. 1998), but these cool-season fires are of lower intensity than those occurring during warm periods (Briggs et al. 2005; Savadogo et al. 2012). This is potentially beneficial for the invasion process as seed mortality from a fire event is a function of intensity and exposure time (Vermeire and Rinella 2009). The dormant season fires, while doing little to reduce the number of seeds, did likely provide increased seed bank exposure through removal of herbaceous material. Native plants may have also initially benefited from these same factors; however, *L. cuneata*'s ability to establish an overwhelming seed bank through high seed production was likely a key factor that facilitated increased *L. cuneata* cover within the most frequently burned (i.e., disturbed) plots.

Invasive *Bromus tectorum* (cheatgrass) has brought significant change to fire behavior across the southwestern United States and resulted in deleterious effects on associated plant and animal communities to the point that recovery of this system is highly unlikely (Whisenant 1990; Knick et al. 2003). Similarly, *Andropogon gayanus* (gamba grass) invasion has produced a drastic increase in both fire frequency and

intensity across the Australian savannas (Rossiter et al. 2003). In both examples, invasive plants have intensified fire characteristics, but elsewhere the opposite has occurred. Keeley (2001) reported the decrease of fire intensities following invasion of annual grasses (*Avena* spp. and *Bromus* spp.) into southern California chaparral and sage scrub systems, while in Australian grasslands invasive shrubs (*Mimosa* spp.) exerted similar negative influence on both fire frequency and extent (Braithwaite et al. 1989).

Across expansive areas in the central and eastern United States now invaded by *L. cuneata*, a similar suppressive effect on fire behavior (see Keeley 2001 and Braithwaite et al. 1989) may occur as invasions progress. The tendency for *L. cuneata* to reduce graminoid cover in invaded areas is the primary cause since graminoids are important fine fuels that influence fire characteristics and alteration of this balance will likely result in decreased fire intensity (Fuhlendorf et al. 1996; Scholes and Archer 1997). Couple this with the relatively recent push to reintroduce fire to grasslands where suppression has allowed initial shrub and woody encroachment (e.g., from *Juniperus virginiana* and *Rhus* spp.) and the conditions are well established for a potentially rapid and unexpected spread of *L. cuneata*.

## **Conclusions**

Invasive species can have a dramatic effect on habitat complexity, structure, and function (Hastings et al. 2007; Gribben et al. 2009). Among these, alterations to fire regimes are documented (e.g., Whisenant 1990; D'Antonio et al. 2000) and produce conditions far different from that under which the native biota evolved (Haferkamp et al. 2001; Hanser and Huntly 2006). My findings illustrate the influence of MFI on *L.*

*cuneata* cover and subsequent negative effects on graminoids (i.e., fine fuels). This finding is unique for *L. cuneata* invasion, but similar results have been reported for shrub and woody grassland invaders; however, compared to *L. cuneata*, considerably more research has examined the underlying processes of fire effects and associated feedbacks related to woody invasion.

Fire reintroduction into grasslands to control shrub and woody plant encroachment should be undertaken with informed caution due to the potential for unexpected and counterproductive results, especially within the range of *L. cuneata* invasion. Many unknowns exist and careful planning and a detailed knowledge of the vegetative community is needed to best guard against further grass- and rangeland loss, especially in non-agricultural areas where large herbivores (i.e., livestock) are absent.

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## Tables

Table 1. Mean fire return interval (MFI; years), related descriptive statistics, and vegetation characteristics for the nine Camp Gruber study plots.

		Plot								
		A	B	C	D	E	F	G	H	I
Fire history data	Coverage years	1953-2006	1956-2007	1966-2010	1918-2005	1921-2008	1926-2008	1933-2010	1971-2007	1981-2010
	Trees sampled (N)	13	12	12	12	12	13	12	12	12
	Fire years (N)	7	10	7	15	8	16	30	8	16
	Fire scars (N)	10	13	13	19	10	20	41	10	24
	MFI <sup>1</sup>	6.1	3.7	4.0	4.3	7.1	3.0	2.2	4.4	1.8
	Min. fire interval	2.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
	Max. fire interval	22.0	20.0	28.0	20.0	28.0	34.0	13.0	7.0	5.0
	Lower exceedance	1.6	0.8	0.7	0.9	1.2	0.4	0.7	2.4	0.8
	Upper exceedance	14.8	10.5	13.6	11.8	23.0	10.9	5.0	6.6	3.1
	Time since fire (yrs.)	7	6	2	8	5	5	2	6	2
Veg. Data	Plant species (N)	68	51	51	62	59	59	56	58	42
	Mean plant richness <sup>2</sup>	8.0 <sup>a</sup>	6.2 <sup>b</sup>	5.2 <sup>cd</sup>	5.8 <sup>bc</sup>	5.9 <sup>bc</sup>	5.5 <sup>bcd</sup>	5.4 <sup>bcd</sup>	6.0 <sup>bc</sup>	4.8 <sup>d</sup>
	<i>L. cuneata</i> cover <sup>3</sup>	0.5	25.4	15.0	16.1	0.9	26.0	18.4	4.5	31.9
	<i>L. cuneata</i> category	Low	High	Mid	Mid	Low	High	Mid	Low	High

<sup>1</sup> Weibull median intervals used; <sup>2</sup> Means with the same letter do not significantly differ ( $P > 0.05$ ); <sup>3</sup> mean cover (% / m<sup>2</sup>)

Table 2. Correlation coefficients and associated *P* values for the relationships between mean *L. cuneata* cover estimates and vegetation and ground cover data. Significant *P* values ( $\leq 0.05$ ) are indicated in ***bold italics***.

Parameter <sup>1</sup>	<i>L. cuneata</i> cover class					
	Low (< 5%)		Mid (15-20%)		High (> 25%)	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
BG	0.22	0.27	0.31	0.12	0.67	< <b><i>0.001</i></b>
RG	0.09	0.63	-0.18	0.34	-0.12	0.55
GL	-0.12	0.55	0.02	0.92	-0.37	<b><i>0.05</i></b>
VR	-0.23	0.25	-0.18	0.37	-0.33	0.11
GRAM	0.09	0.66	-0.37	0.06	-0.59	< <b><i>0.001</i></b>
FORB	0.17	0.40	-0.16	0.43	-0.02	0.92
SHRUB	-0.26	0.19	-0.15	0.46	-0.65	< <b><i>0.001</i></b>
MFI	-0.09	0.66	-0.40	<b><i>0.04</i></b>	-0.62	< <b><i>0.001</i></b>

<sup>1</sup>BG = mean occurrence of bare ground; RG = mean occurrence of rock or gravel; GL = grass litter; VR = total vegetation richness; GRAM = mean graminoid cover; FORB = mean forb cover; SHRUB = mean shrub cover; MFI = mean fire interval

# Figures

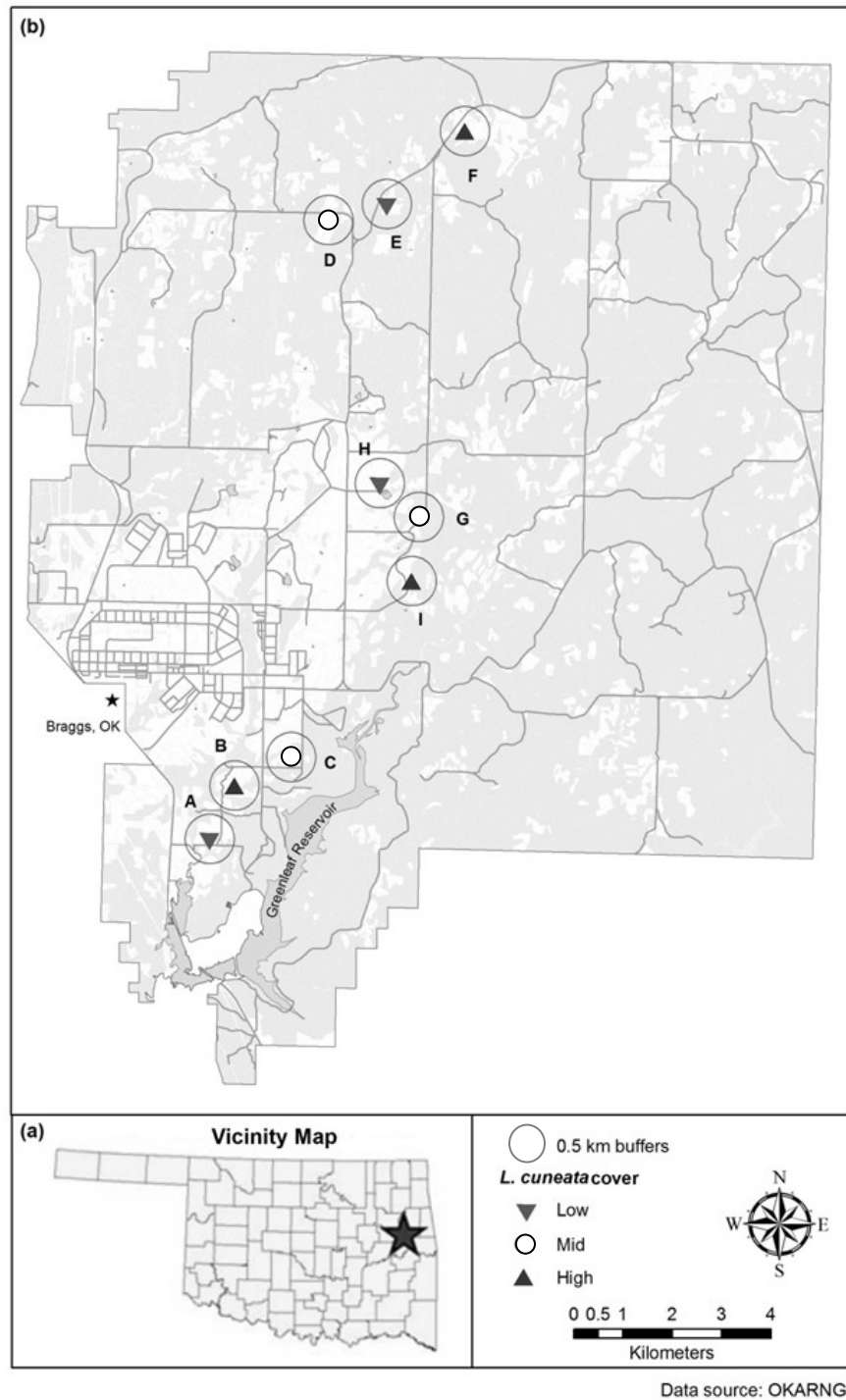


Figure 1. Map of Camp Gruber vicinity (a) and *Q. stellata* and vegetation sampling plots (b).

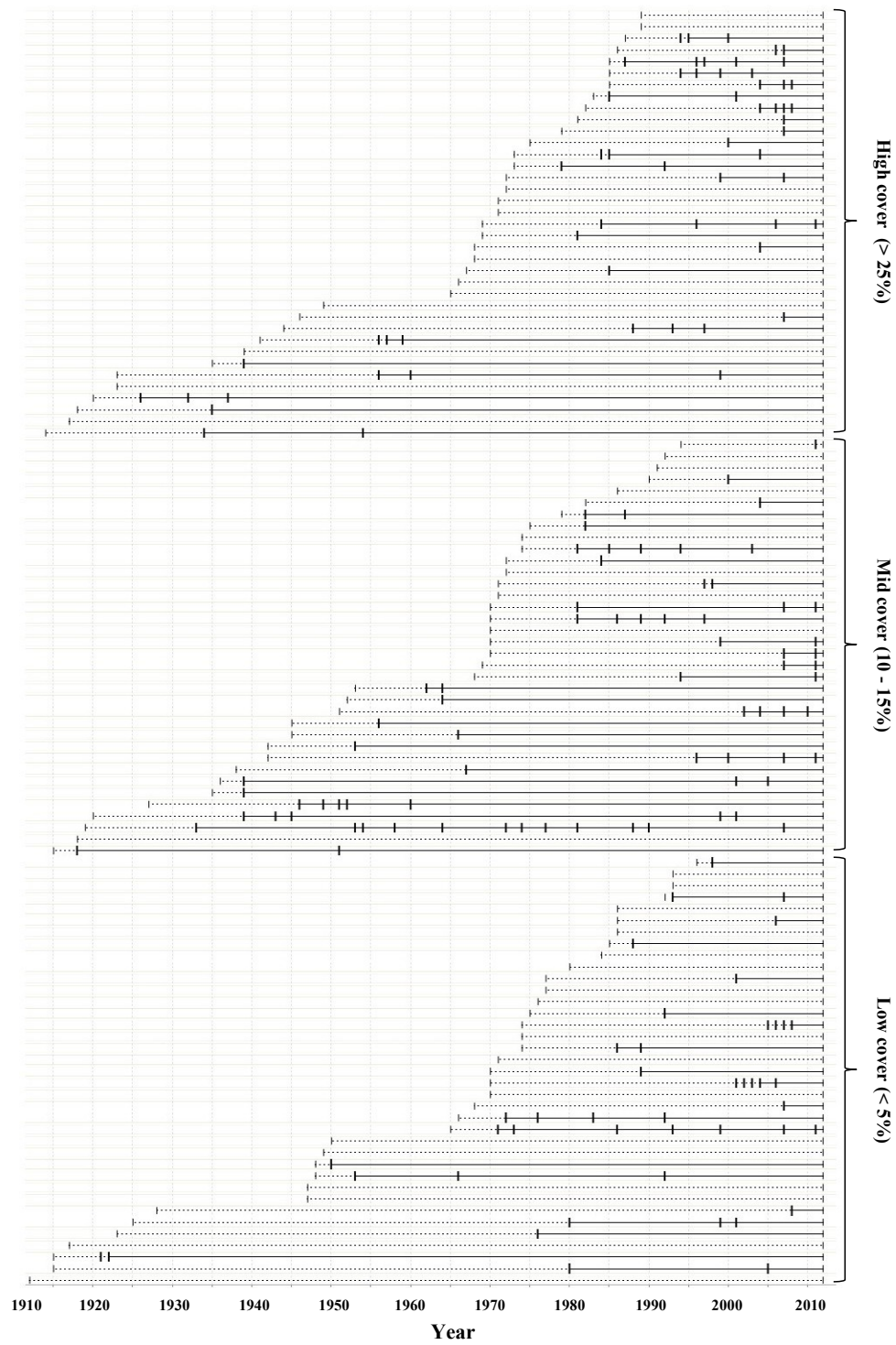


Figure 2. Fire history chart for the nine Camp Gruber study plots combined by *L. cuneata* cover class. Each horizontal line represents an individual *Q. stellata* sampled, while the dark vertical lines represent recorded fire events.



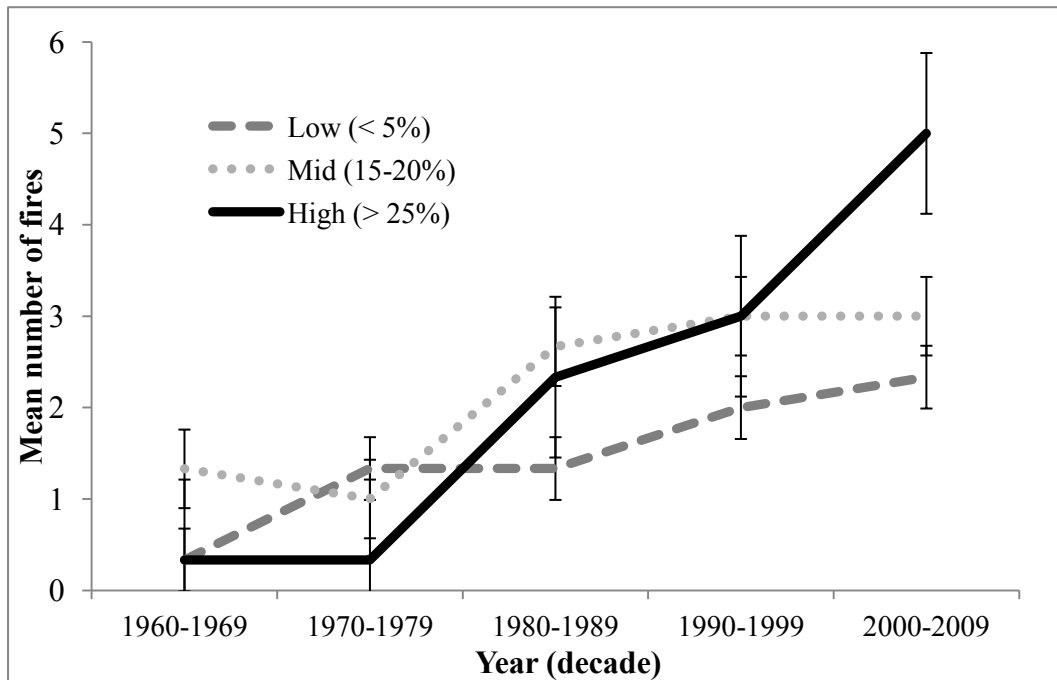


Figure 3. Mean number of fires per decade within the three tested *L. cuneata* cover classes with 5% standard error bars.

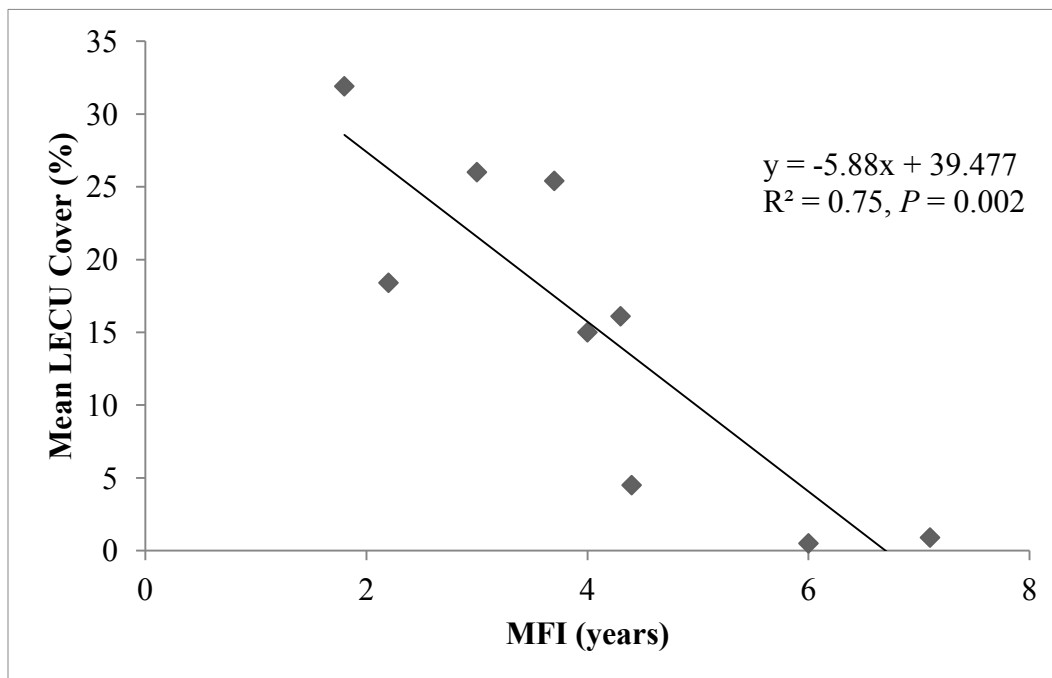


Figure 4. Relationship between mean *L. cuneata* (LECU) cover observed in test plots and the corresponding plot mean fire return interval (MFI). The proportional *L. cuneata* variable was arcsine transformed prior to analysis.

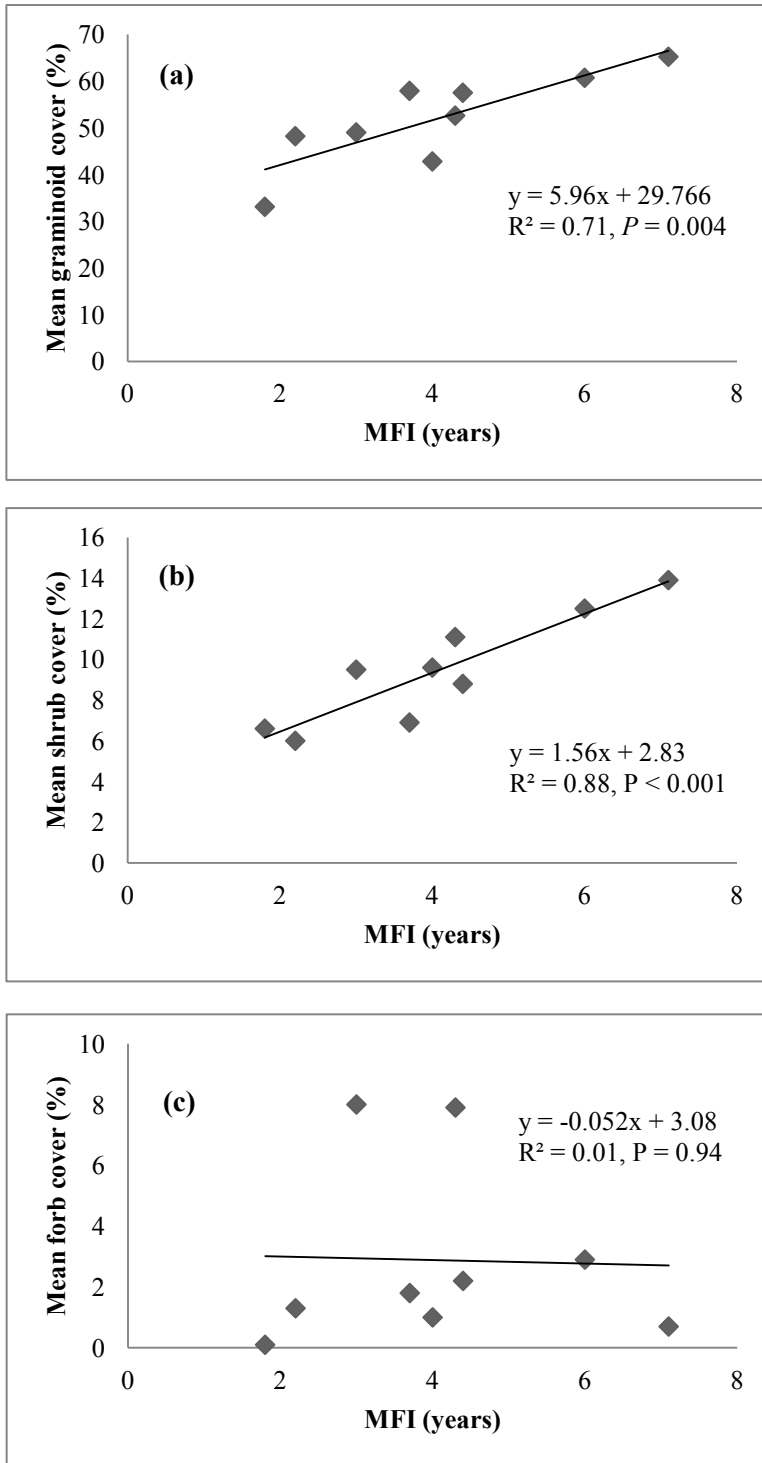


Figure 5. Relationship between mean fire return interval (MFI) and mean graminoid (a), shrub (b), and forb (c) cover. The proportional dependent variables were arcsine transformed prior to analysis.

## APPENDIX

Location and related information for *Quercus stellata* specimens collected to construct the plot-specific Camp Gruber fire history assessment.

Plot	X <sup>1</sup>	Y <sup>1</sup>	Tag #	DBH (cm)	10cm Diameter (cm)	Aspect	Elevation (m)	Slope (%)	Pith Year	Age <sup>2</sup>
A	303195.8	3946395.3	11	21.5	33.8	SW	172	1	1993	20
A	303145.0	3946500.1	12	21.7	34.2	NW	168	1	1991	22
A	303056.2	3946402.6	13	19.2	26.6	W	161	2	1986	27
A	303393.5	3946281.1	14	18.5	25	E	169	1	1993	20
A	303357.0	3946625.6	15	15.5	21.2	NE	159	4	1974	39
A	303440.0	3946487.9	16	10.9	15.8	N	161	0	1985	28
A	303075.5	3946021.6	17	30.4	39.6	W	162	3	1948	65
A	302834.5	3946084.2	18	26.6	32.1	S	152	1	1980	33
A	303136.2	3946084.2	19	26.9	36.3	SW	157	1	1977	36
A	303599.6	3946067.0	31	9.1	12.6	NNW	177	4	1977	36
A	303598.5	3946066.3	32	18	25.5	NNW	177	4	1975	38
A	303479.7	3945863.7	33	21	32.2	W	182	12	1912	101
A	303368.8	3945753.4	34	14.5	21.4	NW	169	7	1947	66
B	303929.2	3947623.6	1	17.5	23.7	N	181	7	1989	24
B	303977.4	3947667.4	2	16.5	22.3	N	178	5	1972	41
B	303562.0	3947615.0	3	24.8	34.9	NW	163	4	1973	40
B	303391.4	3947633.0	4	16.4	23.5	NNE	156	3	1971	42
B	303812.9	3947031.4	5	20.2	30.4	NW	168	5	1975	38
B	303435.3	3947024.1	6	17.1	22.6	NE	170	0	1983	30
B	303390.1	3947174.3	7	24.5	32	SSW	172	1	1979	34
B	303451.2	3947265.8	8	22.3	25.9	W	170	0	1971	42
B	303562.4	3947399.5	9	14.8	18.4	W	158	4	1968	45
B	303986.2	3947456.9	10	28.5	39	SE	178	0	1941	72
B	304135.9	3947203.6	29	25.1	32.9	SW	182	1	1981	32
B	304113.3	3947163.8	30	22.8	30.7	W	183	2	1973	40
C	304514.4	3947625.3	20	21.5	31.5	NNW	194	6	1982	31
C	304720.6	3947701.2	21	22.7	35.4	WNW	202	4	1968	45
C	304733.3	3947530.2	22	14.7	21.4	ESE	197	4	1992	21
C	305040.6	3947571.8	23	19.1	31	NNW	216	7	1951	62
C	304851.0	3947380.5	24	17.8	27.1	SE	201	9	1972	41
C	304960.7	3947658.2	25	44.6	54.6	WNW	206	3	1945	68
C	304544.6	3947973.9	26	16.6	20.5	N	182	1	1971	42
C	304482.9	3947941.6	27	14.6	21.1	N	171	2	1970	43
C	304636.0	3947861.0	28	20	26.9	S	195	1	1970	43

Plot	X <sup>1</sup>	Y <sup>1</sup>	Tag #	DBH (cm)	10cm Diameter (cm)	Aspect	Elevation (m)	Slope (%)	Pith Year	Age <sup>2</sup>
C	305078.0	3947837.9	35	12.6	18.3	SW	210	3	1994	19
C	304807.7	3947922.0	36	25.5	33.8	N	204	2	1970	43
C	304907.8	3948227.9	37	15.2	22.5	NW	195	3	1991	22
D	305959.7	3958874.4	67	18.5	25.2	N	284	2	1945	68
D	305946.9	3958519.2	68	23.3	32.2	W	277	1	1935	78
D	305322.9	3958962.2	69	18.2	25.9	W	280	4	1936	77
D	305388.8	3958703.9	70	28.9	32.2	SSW	279	1	1975	38
D	305592.9	3958634.7	75	14.2	21	E	278	0	1986	27
D	305680.7	3958323.7	76	34.6	39.8	SE	271	4	1920	93
D	305303.8	3958445.2	77	16.4	19.6	S	273	5.5	1974	39
D	305445.0	3958474.4	78	22.7	29.1	SSW	272	0	1979	34
D	305381.5	3958979.9	79	13.5	18.8	NW	285	3	1990	23
D	305438.1	3959115.3	80	24	33.8	W	291	8	1915	98
D	305723.8	3958931.7	83	18.8	27	W	289	4	1953	60
D	305747.0	3959126.4	84	35.7	42.8	ESE	290	4	1942	71
E	306641.4	3959328.1	91	26.6	36.4	SW	291	5	1925	88
E	306533.3	3959100.0	92	14	23.9	WSW	281	5	1986	27
E	306532.3	3958863.9	93	20.4	29.6	WSW	282	1	1915	98
E	306410.9	3958710.3	94	24.8	34.5	W	263	10	1915	98
E	306891.3	3959154.7	100	20.8	27	S	285	2	1948	65
E	307122.3	3959189.5	101	18.8	22.1	E	283	2	1947	66
E	306904.0	3959440.9	102	13.6	19.1	NE	295	1	1950	63
E	306576.7	3959145.8	103	18	24.1	SW	282	1	1975	38
E	306617.3	3958847.1	104	19.7	24.4	SSE	274	1	1923	90
E	306856.1	3958826.9	105	18.5	25.9	S	278	2	1928	85
E	307156.1	3958838.9	106	32.5	41.1	WNW	275	3	1917	96
E	307021.8	3958899.4	107	12.3	16.8	E	280	3	1984	29
F	308001.6	3960461.1	86	10.7	18.4	NNW	259	3	1987	26
F	307857.4	3960462.9	87	20.9	29	NE	268	2	1986	27
F	307822.9	3960491.7	88	13.4	19.9	NE	267	4	1989	24
F	307915.9	3960449.2	89	24.8	33.2	SE	256	7	1982	31
F	307918.7	3960236.5	90	24.7	38.7	NE	266	6	1914	99
F	308469.1	3960189.3	95	25.8	41	N	252	8	1923	90
F	308439.5	3960163.5	96	9.5	12.6	N	255	12	1939	74
F	308399.0	3960150.0	97	18	26.1	N	263	7	1935	78
F	308392.7	3960150.1	98	11.5	18	N	263	5	1949	64
F	307923.0	3960336.5	99	19.7	27.5	N	253	2	1946	67
F	308388.8	3960122.1	108	16.5	23.5	N	266	6	1918	95
F	308427.4	3960152.4	109	13.8	19.2	N	257	3	1923	90
F	308461.7	3960170.2	110	16.7	25.1	N	262	6	1920	93

Plot	X <sup>1</sup>	Y <sup>1</sup>	Tag #	DBH (cm)	10cm Diameter (cm)	Aspect	Elevation (m)	Slope (%)	Pith Year	Age <sup>2</sup>
G	307321.0	3952449.5	38	14.7	22	SSE	230	5	1974	39
G	307220.0	3952502.4	39	18.3	25.9	S	233	4	1970	43
G	307043.2	3952507.7	40	23	31.8	W	214	4	1969	44
G	307495.4	3952389.4	42	25.2	36	SE	229	4	1919	94
G	307421.1	3952762.4	46	17.3	26.5	SW	233	3.5	1970	43
G	307122.5	3952798.8	47	13.5	17.6	NW	209	2	1972	41
G	307544.7	3952552.0	48	11.5	17.7	SE	233	7	1937	76
G	307492.4	3952243.3	49	25	36.7	E	221	4.5	1918	95
G	307307.8	3953134.7	62	19.4	25.9	SW	199	8	1952	61
G	307479.3	3952776.4	63	18.9	26.5	NNE	237	8	1971	42
G	307477.3	3952690.0	64	24	34.2	WNW	234	3	1942	71
G	307498.3	3953104.8	65	22	30	NE	210	3	1927	86
H	306538.4	3953482.7	41	22.6	30	NW	208	6	1970	43
H	306450.2	3953391.8	43	20.8	29.5	NW	199	1	1974	39
H	306391.4	3953488.4	44	15.9	23.3	NE	196	1	1996	16
H	306548.7	3953393.5	45	25	31.8	S	208	2	1970	43
H	306931.2	3953255.5	50	23.7	26.8	SE	198	8	1949	64
H	306881.5	3953096.0	51	23.8	24.9	W	205	2	1966	47
H	306532.3	3952902.1	52	17.8	21.6	NNW	209	0	1992	21
H	306453.5	3952898.7	53	14.6	20	N	209	2	1971	42
H	306781.7	3953621.4	58	12.6	17.5	NNW	210	8	1970	43
H	307055.0	3953342.4	59	13.3	22.6	S	202	3	1968	45
H	306735.3	3953530.2	60	16.8	24.3	N	213	4	1974	39
H	306635.7	3953528.8	61	23.8	36.1	N	209	10	1965	48
I	307143.3	3951632.7	54	26	36.8	S	218	7	1985	28
I	307212.8	3951909.6	55	19	24.1	WNW	222	4	1985	28
I	306850.9	3951760.3	56	25.4	34.1	W	201	1	1972	41
I	307014.0	3951146.0	57	15.6	23.3	W	203	7	1968	45
I	307115.9	3951106.1	66	31.6	38.9	SE	205	13	1965	48
I	307412.7	3951887.9	71	27.1	32.8	SE	221	15	1917	96
I	307233.8	3951466.1	72	31.8	44.4	NW	223	6	1969	44
I	307278.3	3951538.2	73	15.9	18.9	NE	218	11	1967	46
I	307081.4	3951279.6	74	15.9	21.2	SW	210	3.5	1966	47
I	307340.9	3951384.2	81	15	20.2	S	223	2	1985	28
I	307424.9	3951069.0	82	34.2	39.6	E	184	1	1944	69
I	307266.3	3951067.5	85	22.9	29.3	SSW	192	3	1969	44

<sup>1</sup> Universal Transverse Mercator, North American Datum 83; <sup>2</sup> Based on 2012 collection

VITA

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