

Effects of prescribed fire timing on vigor of the invasive forb sericea lespedeza (*Lespedeza cuneata*), total forage biomass accumulation, plant-community composition, and native fauna on tallgrass prairie in the Kansas Flint Hills

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ABSTRACT: The predominant grazing-management practice of the Kansas Flint Hills involves annual prescribed burning in March or April with postfire grazing by yearling beef cattle at a high stocking density from April to August. There has been a dramatic increase in sericea lespedeza (*Lespedeza cuneata* [Dumont] G. Don) coincident with this temporally focused use of prescribed fire in the Flint Hills region. The species is an aggressive invader and a statewide noxious weed in Kansas. Control has generally been attempted using repeated herbicide applications. This approach has not limited proliferation of sericea lespedeza and resulted in collateral damage to nontarget flora and fauna. Alternative timing of prescribed fire has not been evaluated for its control. Our objectives for this 4-yr experiment were to (1) document the effects of prescribed burning during early April, early August, or early September on vigor of sericea lespedeza, standing forage biomass, and basal cover of native graminoids, forbs, and shrubs and (2) measure responses to fire regimes by grassland bird and butterfly communities. Whole-plant dry mass, basal cover, and seed production of sericea lespedeza were markedly less ($P < 0.01$) in

areas treated with prescribed fire in August or September compared with April. Forage biomass did not differ ($P \geq 0.43$) among treatments when measured during July; moreover, frequencies of bare soil, litter, and total basal plant cover were not different ($P \geq 0.29$) among treatments. Combined basal covers of C4 grasses, C3 grasses, annual grasses, forbs, and shrubs also did not differ ($P \geq 0.11$) between treatments. Densities of grasshopper sparrow (*Ammodramus savannarum*), dickcissel (*Spiza americana*), and eastern meadowlark (*Sturnella magna*) were not negatively affected ($P > 0.10$) by midsummer or late-summer fires relative to early-spring fires. There were no differences ($P > 0.10$) in densities of grassland-specialist butterfly species across fire regimes. Under the conditions of our experiment, prescribed burning during summer produced no detrimental effects on forage production, desirable nontarget plant species, grassland birds, or butterfly communities but had strong suppressive effects on sericea lespedeza. Additional research is warranted to investigate how to best incorporate late-summer prescribed fire into common grazing-management practices in the Kansas Flint Hills.

Key words: grassland birds, invasive species, *Lespedeza cuneata*, plant composition, prescribed fire, tallgrass prairie

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INTRODUCTION

Sericea lespedeza (*Lespedeza cuneata* [Dumont] G. Don), a perennial, leguminous forb, was introduced into the United States in the late 19th century from the Sino-Indian region of Asia for its soil conservation properties on farmland and mine spoils, as well as perceived value for wildlife habitat (Mosjidis, 1997). It was introduced into southeastern Kansas in the 1930s to reclaim strip-mined land (Ohlenbusch et al., 2007). In the lag between its introduction and public awareness of its invasive tendencies, sericea lespedeza seed was harvested inadvertently from infested grasslands and unintentionally planted on land enrolled in the U.S. Department of Agriculture Conservation Reserve Program (Eddy et al., 2003); it was also deliberately planted in some Kansas locations (Obermeyer, 2013). The subsequent and continued spread of sericea lespedeza in the tallgrass prairie region is of ongoing concern because it threatens to fundamentally alter one of the most endangered ecosystems on earth (Samson and Knopf, 1994). The Kansas state legislature declared sericea lespedeza a noxious weed in 2000 (Ohlenbusch et al., 2007). To date, sericea lespedeza has heavily degraded approximately 253,000 ha of Kansas rangeland, primarily in the Flint Hills region (KDA, 2018). The resulting damage to pasture quality for domestic herbivores and to native wildlife habitat has been devastating.

Sericea lespedeza tends to be a highly competitive invader in the tallgrass prairie of Kansas for a variety of reasons. Dietary selection of sericea lespedeza growing on native rangelands by beef cattle is limited due to its elevated condensed tannin content (Eckerle et al., 2011; Preedy et al., 2013; Sowers et al., 2019); therefore, control of propagation via grazing is unlikely because pastoral production systems in the tallgrass prairies of Kansas are overwhelmingly dominated by beef cattle (USDA, 2017). When condensed-tannin levels in sericea lespedeza reached 5% to 12% of plant dry matter (DM), depressed DM intake, diet digestibility, and animal productivity were documented

(Aerts et al., 1999). Although cultivated varieties of sericea lespedeza were reported to contain 5% to 8% condensed tannin on a whole-plant DM basis (Mosjidis, 1997), Preedy et al. (2013) documented that condensed-tannin concentration in wild-type sericea lespedeza ranged from 10% to 19% of whole-plant plant DM during the growing season.

Ohlenbusch et al. (2007) speculated that beef cattle avoidance of individual sericea lespedeza plants with naturally greater condensed-tannin concentrations in the Flint Hills region led to natural selection for elevated condensed-tannin levels in wild-type sericea lespedeza. Sericea lespedeza produces both self-fertilizing (i.e., cleistogamous) flowers and flowers that require cross-pollination (i.e., chasmogamous; Donnelly, 1979; Mosjidis, 1997). The latter allow sexual recombination of genetic material between diverse parent plants and are a possible reason why the wild-type plant has adapted relatively quickly to the tallgrass prairie region.

The root system of sericea lespedeza has allelopathic properties that reduce growth and productivity of both cultivated and native grasses (Kalburtji and Mosjidis, 1992; Dudley and Fick, 2003). Sericea lespedeza also tends to produce a robust canopy that prevents sunlight from reaching understory plants, thereby decreasing their photosynthetic potential and carbohydrate synthesis (Ohlenbusch et al., 2007; Vermeire et al., 2007; Allred et al., 2010). Sericea lespedeza can also thrive in shallow and acidic soils that will not support vigorous populations of native plants (Mosjidis, 1997).

In addition, sericea lespedeza is a prolific seed producer (Ohlenbusch et al., 2007). Lemmon et al. (2017) found that single sericea lespedeza stems produced an average of 864 seeds annually over a 4-yr period. Only 40% of newly formed sericea lespedeza seeds with an intact seed coat germinated, whereas 85% germinated when the seed coat was scarified (Logan et al., 1969). Nonscarified sericea lespedeza seed may remain viable in the soil for many years, leading to a prolonged germination interval (Walters et al., 2005; Cummings et al., 2017).

Fire probably plays a critical role in scarification of sericea lespedeza seed. [Herranz et al. \(1998\)](#) indicated that dry or moist heat effectively scarified seeds of seven Leguminosae species. Subsequently, [Vermeire et al. \(2007\)](#) and [Wong et al. \(2012\)](#) indicated that prescribed fire stimulated sericea lespedeza germination.

When fire scarification occurs in early spring, new sericea lespedeza seedlings would be allowed a full growing season to develop robust roots and store carbohydrate reserves, thereby improving survival odds for subsequent growing seasons. We speculated that prescribed burning late during the growing season would limit photosynthetic opportunities for sericea lespedeza seedlings and potentially diminish subsequent survival odds.

In pastoral beef production systems of the tallgrass prairie, sericea lespedeza invasion has manifested itself as diminished carrying capacity for beef cattle grazing ([Preedy et al., 2013](#); [Sowers et al., 2019](#)); however, detrimental effects of invasion on grassland fauna have also been documented. [Eddy and Moore \(1998\)](#) observed diminished invertebrate diversity in sericea lespedeza-invaded tallgrass prairie, whereas [Brooke et al. \(2016\)](#) reported disproportionate placement of nests by northern bobwhite (*Colinus virginianus*) in areas that had been treated with herbicide to control sericea lespedeza compared with areas that were not treated. Controlling the spread of sericea lespedeza is essential not only for the preservation of grazing lands but also for the preservation of native wildlife and native pollinators ([Eddy and Moore, 1998](#)). Therefore, it is imperative that any proposed control practices be assessed for negative effects on endangered grassland fauna ([Potts et al., 2010](#); [Rosenberg et al., 2019](#)).

We hypothesized that annual prescribed burning conducted at a time when sericea lespedeza was flowering or producing seed (i.e., during the latter portion of the growing season) would have suppressive effects on sericea lespedeza vigor (e.g., biomass, seed production) compared with locally conventional, dormant-season, annual prescribed burning. Effects of timing of prescribed fire on nontarget plant species and native wildlife and pollinator communities also merited exploration to completely assess effects of the proposed practice. Therefore, our objective was to evaluate the effects prescribed-burn timing of native tallgrass range on vigor of sericea lespedeza, overall forage production, soil cover, plant species composition, plant species diversity, grassland-nesting songbird and butterfly density, and songbird nest placement.

MATERIALS AND METHODS

Study Area

Our experiment was conducted between March 2014 and November 2017. We used a 50-ha native tallgrass pasture located in Geary County, Kansas (39°18'N, 96°57'W). Soils were of the Benfield-Florence complex with 5% to 30% slope (85% of total area), Kahola silt loam (channeled; 9% of total area), or Tully silty clay loam (1% to 7% slope; 6% of total area; [USDA-NRCS, 2018](#)). Annual precipitation at the site was 630, 901, 1,129, and 758 mm in 2014, 2015, 2016, and 2017, respectively (30-yr mean annual precipitation = 852 mm); 30-yr mean annual temperature was 12.4°C ([KMHW, 2018](#)). The site was historically grazed during winter and early spring by beef cattle.

Treatments

The research site was divided along natural watershed boundaries into nine fire-management units (5 ± 2.6 ha). Burn unit boundaries were delineated by mowing firebreaks (6 m wide) around each perimeter before treatment application. Burn units were assigned randomly to one of three treatments based on timing of prescribed fire ($n = 3$ per treatment): spring (1 April ± 10.7 d), which served as a positive control; midsummer (1 August ± 1.9 d); or late summer (1 September ± 2.7 d). Treatments were applied on or near target dates for four consecutive years. Grazing by domestic herbivores was excluded for the duration of the experiment.

Prescribed burns were carried out only when appropriate environmental conditions prevailed: surface wind speed = 8 to 20 km/h; surface wind direction = steady and away from urban areas; mixing height ≥ 550 m; transport wind speed = 13 to 33 km/h; relative humidity = 40% to 70%; ambient temperature = 13 to 30°C; and Haines index ≤ 4. All prescribed-burning activities were carried out with the permission of Geary County Emergency Services, Junction City, Kansas (permit no. 348).

Vegetation Response

Total forage biomass, sericea lespedeza stem length, and sericea lespedeza aerial frequency were measured twice annually (17 July ± 7.5 d and 10 October ± 3.7 d) along a single, permanent 100-m transect in each fire-management unit. Transects were laid out exclusively on Benfield-Florence complex soils with less than 2% slope. At 1-m intervals along each transect, total standing forage biomass

was estimated using a visual obstruction technique (Robel et al., 1970); biomass estimates were expressed as kg of forage DM/ha. Additionally, a 30 × 30 cm quadrat was placed parallel to the eastern side of transects at 1-m intervals along each transect and the presence of sericea lespedeza was noted. The number of occurrences per 100 observations was expressed as aerial frequency (%) of sericea lespedeza. When sericea lespedeza was present in quadrats, the length of the stem nearest the 1-m interval was recorded in centimeter.

A total of 100 sericea lespedeza stems were collected at randomly selected intervals along permanent transects in each burn-management unit immediately after the first killing frost (average date = 1 November ± 3.2 d). Stems were clipped at ground level, placed into a labeled paper bag, dried to a constant mass in a forced-air oven (50°C; 96 h), and weighed to the nearest mg. Individual stems in each sample were then defoliated manually, with seeds, leaves, chaff, and stems placed collectively into a seed cleaner (Model B, Seedbuco Equipment Co., Des Plaines, IL) to separate seeds. Cleaned seed was weighed to the nearest mg and converted to seed count assuming a density of 770 seeds/g (Vermeire et al., 2007; Vandevender, 2014). Average seed production per stem was calculated by dividing the number of seeds by the number of sericea lespedeza stems in each sample.

In the final year of the experiment, vegetation within 10 randomly placed 0.25-m² quadrats were clipped adjacent to each transect at a height of 1 cm to estimate sericea lespedeza biomass within each burn-management unit. These biomass measurements were conducted on 11 July 2017. Clipped material was hand sorted into sericea lespedeza biomass and nonsericea lespedeza biomass, dried in a forced-air oven (50°C; 96 h), and weighed to the nearest milligram. Estimates of forage biomass were expressed as kg of forage DM/ha.

Plant species composition and soil cover were evaluated annually along each permanent transect in mid-July using a modified step-point technique (Owensby, 1973; Farney et al., 2017). Transect points ($n = 100$ per transect) were evaluated for bare soil, litter cover, or basal plant area (% of total area). Plants were identified to species; basal cover of individual species was expressed as a percentage of total basal plant area. Common and scientific names of plants were taken from Haddock (2005). Comprehensive lists of graminoids, forbs, and shrubs encountered during plant-composition analyses were compiled (Supplementary Appendices 1, 2, and 3, respectively).

Plant species were classified into growth-form categories to evaluate changes in growth-form composition (Hickman et al., 2004). Categories included C4 tall grasses, C4 mid grasses, C4 short grasses, C3 grasses and sedges, annual grasses, perennial forbs, annual forbs, all shrubs, and increaser shrubs (i.e., shrubs that tend to proliferate in response to grazing; Vesik and Westoby, 2001; roughleaf dogwood [*Cornus drummondii*], smooth sumac [*Rhus glabra*], and buckbrush [*Symphoricarpos orbiculatus*]. An additional category we considered consisted of native-leguminous or nectar-producing forbs that were deemed critical to ecosystem function. These were classified as major wildflowers: catclaw sensitive briar (*Mimosa quadrivalvis*); dotted gayfeather (*Liatis punctata*); heath aster (*Symphyotrichum ericoides*); prairie coneflower (*Ratibida columnifera*); purple poppymallow (*Callirhoe involucrate*); purple prairieclover (*Dalea purpurea*); round-headed prairieclover (*Dalea multiflora*); and white prairieclover (*Dalea candida*).

Plant species richness ($S =$ number of species sampled per transect) and evenness ($H'/\ln[S]$, where $H' = -\sum p_i - \ln[p_i]$ and $p_i =$ the proportion of the total plant community comprised of species i) were calculated for each transect using all plant species, native plant species only, grasses only, and forbs only (Magurran, 2004). In addition, Simpson dominance ($D = \sum p_i^2$; i.e., an estimate of the probability of two plants randomly and independently selected from the community belonging to the same species) and Simpson diversity ($-\log D$; i.e., an index positively related to diversity) were calculated using all plants, native plants only, grasses only, and forbs only (Simpson, 1949; Pielou, 1975; Magurran, 2004).

Grassland Bird and Butterfly Response

Estimates of avian density were obtained by conducting 50-m fixed-radius point-count surveys with distance sampling (Buckland et al., 2001). A total of 330 point-count surveys were conducted from mid-May to early June 2015 and 2016. The point-count period began with a 2-min acclimation period, followed by 5 min of survey in which two independent observers recorded the species of each bird detected by sight or sound within the survey area. The distance from the observer to each bird was measured with a Leica Rangemaster CRF 1000-R rangefinder. Point counts were conducted between 0600 and 1045 on mornings with no precipitation and winds ≤ 32 km/h. Each morning, among the point-count stations, a random start

point was generated with subsequent order depending on the nearest neighboring point-count location.

Nests of grassland-nesting songbirds were located via rope-dragging, following females to their nests, and serendipitous flushing from late May to late July 2015 and 2016. Locations of nests were recorded on a handheld GPS and marked by placing two stakes, one 5 m north and one 5 m south, of the nest. Proportional aerial cover of grass, shrubs, forbs, litter, and bare ground were estimated within a 1-m² Daubenmire frame 1-d postfledging or on the anticipated fledge date if the nest had failed, at each monitored grassland songbird nest and a paired unused point 5 m away from the nest. In 2016, proportional canopy coverage of sericea lespedeza was also estimated. Proportions were placed into six classes (0.0 to 0.05, 0.06 to 0.25, 0.26 to 0.50, 0.51 to 0.75, 0.76 to 0.95, and 0.95 to 1.0), and the midpoint of each class was used for analyses (Daubenmire, 1959).

The butterfly (Order Lepidoptera) community was surveyed using a modified Pollard walk method (Pollard, 1977). Surveys were conducted along permanent 100-m transects between 0900 and 1800 on days with no precipitation, winds \leq 24 km/h. All butterflies detected within 5 m of either side of each transect and within 15 m aboveground were recorded and identified to species or lowest possible taxonomic level once monthly from June to September in 2015 and from May to September in 2016. Orange, clouded, and dainty sulphur butterfly species (*Colias eurytheme*, *Colias philodice*, and *Nathalis iole*) were difficult to distinguish without capture; therefore, they were combined as sulphur spp. Likewise, due to the difficulty in distinguishing without capture, spring and summer azures (*Celastrina ladon* and *Celastrina neglecta*) were combined as azure spp., and all species within the Grass Skipper subfamily (Family Hesperiiidae, subfamily Hesperinae) were combined as grass-skipper species.

Statistical Analyses

Total forage biomass, sericea lespedeza aerial frequency, and sericea lespedeza stem length were analyzed as a completely random design using a mixed model (PROC MIXED, SAS Inst. Inc., Cary, NC). Class variables included transect, time (i.e., month of measurement), treatment, and year. Transect within burn unit was the experimental unit. Initial models contained fixed effects for treatment, time, year, treatment \times year,

treatment \times time, and treatment \times time \times year. Treatment \times year and treatment \times time \times year were not significant ($P \geq 0.18$); therefore, final models contained terms for treatment, time, and treatment \times time as fixed effects and year as a repeated measure.

Whole-plant dry mass and seed production of sericea lespedeza were analyzed as completely random designs using a mixed model with transect, treatment, and year as class variables. Transect within burn unit was again the experimental unit. Initial models included fixed effects for treatment, year, and treatment \times year. The interaction term was not significant ($P \geq 0.48$); therefore, the final models contained terms for treatment as a fixed effect and year as a repeated measure. Clipped sericea lespedeza biomass was analyzed as a completely random design (PROC MIXED, SAS Inst. Inc.). Class statements included transect, treatment, and observation. Transect was the experimental unit, and observation within transect was considered a repeated measure.

Frequencies of bare soil, litter, total basal vegetation, basal cover of growth-form categories, and diversity measures were analyzed as a completely random design using a mixed model (PROC MIXED, SAS Inst. Inc.). Class variables were year, treatment, and transect. Transect within burn unit was the experimental unit. Initial models included fixed effects for treatment, year, and treatment \times year. Treatment \times year was not significant ($P \geq 0.48$); therefore, the final models contained fixed effects for treatment and year was considered a repeated measure.

When protected by a significant F -test ($P \leq 0.05$), least-squares means for treatment and treatment \times time were separated using the method of least significant difference.

Avian detection probabilities and densities were calculated using Program Distance (version 6.2 Release 1; Thomas et al., 2010). Detection probabilities and densities were estimated separately for grasshopper sparrow (*Ammodramus saviarum*), dickcissel (*Spiza americana*), and eastern meadowlark (*Sturnella magna*), the focal grassland-nesting birds. Observations from 2015 and 2016 were right-truncated at 50 m and pooled between year. Detection functions were calculated using a half-normal key function and a cosine series expansion. Densities were poststratified by species; we compared rankings of a model using treatment as a covariate to a model without any covariates (i.e., null model). Models were ranked using Akaike's information criterion, corrected for small sample size (AIC_c; Burnham and Anderson, 2002). In

comparing a density model considering fire treatment to the null model, the treatment model outperformed the null model by >1900 AIC_c units, with 100% of the weight; therefore, only results from the treatment model are reported here. Differences in avian and butterfly density among fire treatments were tested using chi-square analyses in Program CONTRAST (version 2.0; Hines and Sauer, 1989). We calculated diversity of the butterfly community using Shannon's Diversity Index.

We compared aerial cover measurements between nests and random points using Wilks' lambda multivariate analysis of variance (MANOVA) tests in Program R (version 3.1.1; R Development Core Team, 2010) and subsequent completely random design ANOVA and Tukey's HSD tests following a significant MANOVA ($P < 0.05$) to separate treatments for each dependent variable. Proportional canopy coverage of grass, forbs, litter, and bare ground were included as dependent variables for the aerial cover MANOVA. Differences in proportional aerial cover of sericea lespedeza between nesting points or paired, random points in 2016 were tested using a completely random design ANOVA.

RESULTS AND DISCUSSION

Standing Forage Biomass

Standing forage biomass was influenced ($P < 0.01$; Figure 1) by treatment and measurement time. Standing forage biomass did not differ ($P \geq 0.43$) between treatments in July. Abrams et al. (1986) indicated that aboveground biomass on Kansas tallgrass prairie peaked in mid to late July during a 10-yr experiment. We concluded that repeated burning late in the growing season did not

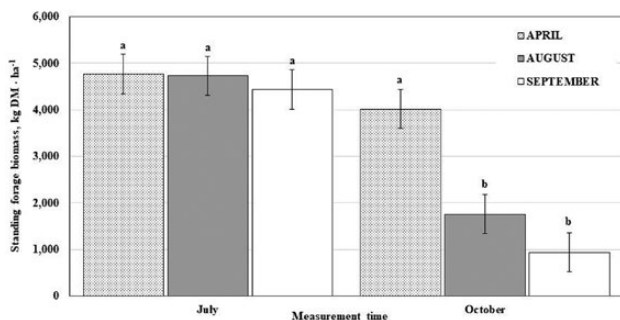


Figure 1. Effects of the timing of annual prescribed burning of native tallgrass prairie on average standing forage biomass estimated on 17 July \pm 7.5 d and 10 October \pm 3.7 d (treatment \times time – $P < 0.01$). The research site was divided along natural watershed boundaries into nine fire-management units (5 ± 2.6 ha). Burn units were assigned randomly to one of three prescribed-burning times: April (1 April \pm 10.7 d); August (1 August \pm 1.9); or September (1 September \pm 2.7 d). Treatments were applied on or near target dates from 2014 to 2017. Means with unlike superscripts differ ($P \leq 0.05$).

impair forage production compared with conventional spring burning.

In October, forage biomass was greater ($P < 0.01$) in areas burned in early spring compared with those treated with prescribed fire in August or September (Figure 1). Prescribed fire in August and September removed nearly all of aboveground plant material; however, forage regrowth following fires resulted in substantial accumulation of biomass prior to seasonal plant dormancy. Standing forage biomass in areas treated with prescribed fire in early spring decreased by an average of 752 kg/ha (18.7%) between July and October. By comparison, standing forage biomass in areas treated with prescribed fire in August and September recovered to 37% and 21%, respectively, of prefire standing forage biomass levels during the period between treatment application and October. We concluded that postfire regrowth was probably sufficient to prevent erosion during the subsequent dormant season and any treatment differences in soil moisture loss that may have occurred were insufficient to impair subsequent forage yields.

Average forage regrowth on watersheds treated with prescribed fire during August in our experiment (1,761 kg/ha) was sufficient to allow light to moderate grazing during the ensuing fall and winter, whereas postfire regrowth on watersheds treated with prescribed fire during September (935 kg/ha; Figure 1) was less substantial. Aboveground net primary production of grasses did not differ when native tallgrass watersheds were burned frequently over a 20-yr period in November, February, or April and soil moisture losses were not different across fire regimes (Towne and Craine, 2014).

Standing biomass of sericea lespedeza was estimated using a clipping technique during the final year of our experiment. The intent was to measure the cumulative effects of prescribed fire in April, August, or September on sericea lespedeza biomass as a proportion of total standing forage biomass. Biomass estimates were conducted 91 d after the April burn and 22 and 50 d prior to the August and September burns, respectively, in July 2017. Biomass of sericea lespedeza was greater ($P < 0.01$; Figure 2) in the April treatment than either the August or September treatments. Total standing forage biomass was greater ($P < 0.01$) in the April and August burn treatments compared with the September burn treatment; however, nonsericea lespedeza standing biomass did not differ ($P = 0.88$) between April and September burn treatments and was greater ($P < 0.01$) in the August burn treatment than in the April or September burn treatments.

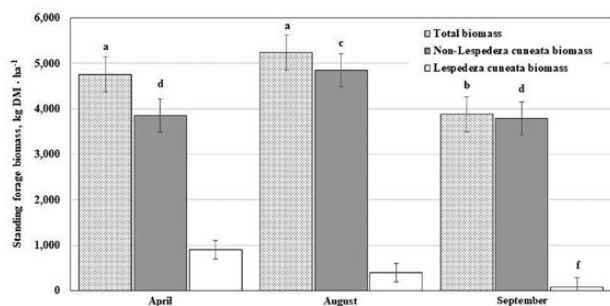


Figure 2. Effects of the timing of annual prescribed burning of native tallgrass prairie on total standing forage biomass, sericea lespedeza (*Lespedeza cuneata*) biomass, and nonsericea lespedeza biomass during August 2017 following four consecutive years of annual burning on nine fire-management units (5 ± 2.6 ha) in the Kansas Flint Hills. Burn units were assigned randomly to one of three prescribed-burning times: April (1 April ± 10.7 d); August (1 August ± 1.9 d); or September (1 September ± 2.7 d). Treatments were applied on or near target dates from 2014 to 2017. Within biomass category, means with unlike superscripts differ ($P \leq 0.05$).

Biomass of sericea lespedeza in the April treatment was estimated at 901 kg/ha, or 19% of total biomass, whereas biomasses of sericea lespedeza in August and September fire treatments were estimated to be 394 kg/ha (8% of total biomass) and 86 kg/ha (2% of total biomass), respectively (Figure 2). Allred et al. (2010) reported that sericea lespedeza had 130% more aboveground biomass at the end of the growing season than big bluestem (*Andropogon gerardii*), clearly underscoring the competitive capabilities of sericea lespedeza in relation to plant species characteristic of the tallgrass prairie.

When aboveground plant biomass decreases, root production is expected to decrease concomitantly (Jameson, 1963). In our experiment, an increase in aboveground sericea lespedeza biomass in the April prescribed-fire treatment may have been associated with increased sericea lespedeza root biomass and decreased root biomass of native plants. Partial defoliation of sericea lespedeza achieved through grazing late in the growing season resulted in reduced aboveground sericea lespedeza biomass (Pacheco et al., 2012; Preedy et al., 2013; Lemmon et al., 2017). Nearly complete defoliation of sericea lespedeza, achieved through annual prescribed burning late in the growing season in our experiment, may have resulted in progressively depressed sericea lespedeza root carbohydrate reserves, mortality of some mature sericea lespedeza plants, and less robust surviving sericea lespedeza plants.

Sericea Lespedeza Vigor

Diminished vigor of sericea lespedeza in response to prescribed fire conducted during August

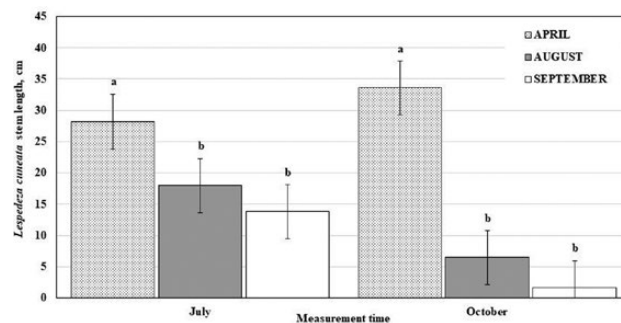


Figure 3. Effects of the timing of annual prescribed burning of native tallgrass prairie on stem length of sericea lespedeza (*Lespedeza cuneata*) measured on 17 July ± 7.5 d and 10 October ± 3.7 d (treatment \times time – $P < 0.01$). The research site was divided along natural watershed boundaries into nine fire-management units (5 ± 2.6 ha) in the Kansas Flint Hills. Burn units were assigned randomly to one of three prescribed-burning times: April (1 April ± 10.7 d); August (1 August ± 1.9 d); or September (1 September ± 2.7 d). Treatments were applied on or near target dates from 2014 to 2017. Means with unlike superscripts differ ($P \leq 0.05$).

and September was suggested by our measurements of sericea lespedeza stem length, aerial frequency, whole-plant dry mass, and seed production. Treatment and measurement time influenced ($P < 0.01$; Figure 3) sericea lespedeza stem length. Mean stem length in areas treated with prescribed fire in April did not change ($P = 0.21$) between July and October and was greater ($P \leq 0.02$) than mean sericea lespedeza stem length in areas treated with prescribed fire in August or September. Within measurement date, mean sericea lespedeza stem length did not differ ($P \geq 0.27$) between the August and September fire treatments.

At the outset of the study, aerial frequency of sericea lespedeza on all transects averaged $36 \pm 3.4\%$ and did not differ ($P = 0.89$; data not shown) among treatments. Subsequently, aerial frequency of sericea lespedeza was not influenced by time of measurement (Table 1). Aerial frequency of sericea lespedeza was least ($P < 0.01$) in September burn units (18.0% of all 30×30 cm plots), intermediate in August burn units (30.8% of plots), and greatest in April burn units (53.0% of plots).

Once established, sericea lespedeza typically grows taller than competing native plants and tends to have a dense, branching aerial structure that can prevent sunlight from reaching understory plants (Ohlenbusch et al., 2007; Vermeire et al., 2007; Allred et al., 2010). Leaf area is critical for plant growth and carbon assimilation (Reich et al., 1997); moreover, sericea lespedeza had greater leaf area in proportion to total plant mass than competing native plants during the latter part of the growing season (Allred et al., 2010). In our experiment, prescribed fire applied in August or September limited

Table 1. Effects of timing of annual prescribed burning of native tallgrass prairie in *Lespedeza cuneata* aerial frequency, whole-plant dry mass at dormancy, and seed production and on occurrence of bare soil, litter, and total basal vegetation cover in nine fire-management units (5 ± 2.6 ha) in the Kansas Flint Hills

Item	Prescribed-burn time			SEM ¹
	April	August	September	
Aerial frequency, % of all plots	53.0 ^a	30.8 ^b	18.0 ^c	5.43
Whole-plant mass, mg DM/stem	3,815 ^a	446 ^b	130 ^b	452.70
Seed production, seeds/stem	590.3 ^a	25.3 ^b	0.3 ^b	139.42
Bare soil, % total area	39.4	43.3	39.5	8.80
Litter cover, % total area	50.7	47.4	49.6	9.04
Basal vegetation cover, % total area	9.9	9.3	10.9	1.05

Burn units were assigned randomly to one of three prescribed-burning times: April (1 April \pm 10.7 d); August (1 August \pm 1.9); or September (1 September \pm 2.7 d). Treatments were applied on or near target dates from 2014 to 2017.

¹Mixed-model SEM associated with comparison of treatment main-effect means.

^{a,b,c}Within rows, means with unlike superscripts differ ($P \leq 0.05$).

the canopy-dominating qualities of sericea lespedeza compared with prescribed fire applied in April and may have allowed native plants to opportunistically colonize soil and canopy space formerly occupied by sericea lespedeza.

Whole-plant dry mass of sericea lespedeza and seed production per sericea lespedeza stem, both assessed annually immediately after the first killing frost, were greatly diminished ($P < 0.01$) in areas treated with prescribed fire in August or September compared with areas treated in April (Table 1). Seed production in the August treatment was approximately 4% of that in April treatment. In the September treatment, seed production was approximately 0.05% that of the April treatment. Sericea lespedeza is a prolific seed producer (Ohlenbusch et al., 2007); moreover, seed is the means by which it spreads geographically. Therefore, control or elimination of seed production may significantly slow the rate of invasion of sericea lespedeza in tallgrass prairie plant communities.

Walters et al. (2005) and Cummings et al. (2017) reported that sericea lespedeza seeds had remarkable durability in the soil. This begs the question of the fate of existing sericea lespedeza seeds

in the soil bank. Vermeire et al. (2007) indicated that prescribed burning during spring stimulated germination of sericea lespedeza seed within the soil bank by scarifying the seed coat. Under these circumstances, seedlings would be afforded a full growing season to store root carbohydrate reserves and improve survival odds for subsequent year. The timing of fire, however, may not be the critical issue. It is reasonable to assume that prescribed fire during any season could promote sericea lespedeza seed germination (Herranz et al., 1998; Wong et al., 2012). We speculated that seed germination occurring late during the growing season would limit photosynthetic opportunities for seedlings and potentially diminish over-winter survival odds. Reduction in sericea lespedeza aerial frequency observed in our experiment may be partially explained by mortality of seedlings that initiated growth late in the growing season.

Soil Cover and Plant Species Composition

Frequencies of bare soil, litter, and total basal vegetation did not differ ($P \geq 0.29$) among April, August, and September prescribed-fire treatments (Table 1). Values reported in our experiment were generally indicative of healthy tallgrass prairie ecosystems (Fuhlendorf and Engle, 2004). Basal-cover values for all graminoids and basal-cover values for individual graminoids growth-form classifications did not differ ($P \geq 0.51$; data not shown) among treatments before our experiment began. At the conclusion of our study, basal-cover values for all graminoids, C4 perennial grasses, C3 grasses and sedges, and annual grasses were also not different ($P \geq 0.11$) among treatments (Table 2).

In contrast, we observed shifts in basal cover among growth forms within the C4 grasses (Table 2). Cumulative basal cover of C4 tall grasses (i.e., big bluestem, eastern gamagrass [*Tripsacum dactyloides*], Indiangrass [*Sorghastrum nutans*], purpletop [*Tridens flavus*], sand paspalum [*Paspalum setaceum*], and switchgrass [*Panicum virgatum*]) was greater ($P < 0.01$) in areas burned for four consecutive years in April and August than in areas burned in September. This change was accompanied by an increase in C4 midgrasses in the September burn treatment compared with April and August burn treatments ($P < 0.01$). Areas burned in August also had slightly less ($P = 0.04$) C4 perennial short grass basal cover than areas burned in April or September.

To evaluate the nature of the shift in basal cover between C4 tall grass and C4 midgrass

Table 2. Effects of the timing of annual prescribed burning on basal vegetation cover on native tallgrass prairie in nine fire-management units (5 ± 2.6 ha) in the Kansas Flint Hills

Item, % basal plant cover	Prescribed-burn time			SEM ¹
	April	August	September	
Total grass cover	82.8	85.9	86.5	2.17
C4 grasses	67.7	65.9	64.8	3.40
C4 tall grasses ²	36.2 ^a	41.1 ^a	22.1 ^b	3.52
<i>Andropogon gerardii</i>	18.4 ^a	18.1 ^a	11.9 ^b	2.61
<i>Sorghastrum nutans</i>	12.1 ^{ab}	15.0 ^a	9.4 ^b	2.13
<i>Panicum virgatum</i>	5.5	4.0	1.5	1.70
C4 midgrasses ³	28.2 ^a	23.7 ^a	39.3 ^b	3.48
<i>Schizachyrium scoparium</i>	14.2 ^a	11.8 ^a	23.0 ^b	3.76
<i>Bouteloua curtipendula</i>	9.9	7.4	11.0	3.27
C4 short grasses ⁴	3.3 ^a	1.1 ^b	3.4 ^a	1.00
C3 grasses and sedges ⁵	15.1	19.7	21.7	3.11
Annual grasses ⁶	0.1	0.3	0	0.23
Total forb cover	15.4	12.1	11.2	2.28
Perennial forbs	15.3 ^a	10.9 ^b	9.7 ^b	2.05
Major wildflowers ⁷	0.56 ^a	0.88 ^{ab}	1.35 ^b	0.283
<i>Lespedeza cuneata</i> ⁸	7.27 ^a	3.38 ^b	1.72 ^b	1.560
<i>Vernonia baldwini</i> ⁹	0.71 ^a	0.22 ^b	0.38 ^b	0.156
<i>Ambrosia psilostachya</i> ¹⁰	3.29 ^a	0.93 ^b	0.73 ^b	0.534
Annual forbs	0.05 ^a	1.21 ^b	1.45 ^b	0.517
Total shrub cover	1.80	1.93	2.34	0.476
Increase shrubs ¹¹	0.98 ^a	0.46 ^b	0.85 ^a	0.204
<i>Amorpha canescens</i> ¹²	0.79	1.27	1.41	0.415
<i>Ceanothus americanus</i> ¹³	0 ^a	0.19 ^b	0.01 ^a	0.063

Burn units were assigned randomly to one of three prescribed-burning times: April (1 April \pm 10.7 d); August (1 August \pm 1.9); or September (1 September \pm 2.7 d). Treatments were applied on or near target dates from 2014 to 2017.

¹Mixed-model SEM associated with comparison of treatment main-effect means.

²Combined basal cover of big bluestem (*Andropogon gerardii*), eastern gamagrass (*Tripsacum dactyloides*), Indiangrass (*Sorghastrum nutans*), purpletop (*Tridens flavus*), sand paspalum (*Paspalum setaceum*), and switchgrass (*Panicum virgatum*).

³Combined basal cover of fall witchgrass (*Digitaria cognata*), little bluestem (*Schizachyrium scoparium*), purple lovegrass (*Eragrostis spectabilis*), sideoats grama (*Bouteloua curtipendula*), and tall dropseed (*Sporobolus asper*).

⁴Combined basal cover of blue grama (*Bouteloua gracilis*), buffalograss (*Bouteloua dactyloides*), hairy grama (*Bouteloua hirsuta*), and tumble windmillgrass (*Chloris verticillata*).

⁵Combined basal cover of Canada wildrye (*Elymus canadensis*), Japanese brome (*Bromus japonicus*), Kentucky bluegrass (*Poa pratensis*), prairie junegrass (*Koeleria macrantha*), sedges (*Carex* spp.), Scribner panicum (*Dichantheium oligosanthos*), and Virginia wildrye (*Elymus virginicus*).

⁶Combined basal cover of Japanese brome (*Bromus japonicus*) and prairie threeawn (*Aristida oligantha*).

⁷Combined basal cover of catclaw sensitive briar (*Mimosa quadrivalvis*), dotted gayfeather (*Liatrix punctata*), heath aster (*Symphyotrichum ericoides*), prairie coneflower (*Ratibida columnifera*), purple poppymallow (*Callirhoe involucrata*), purple prairieclover (*Dalea purpurea*), round-headed prairieclover (*Dalea multiflora*), and white prairieclover (*Dalea candida*).

⁸Sericea lespedeza.

⁹Baldwin's ironweed.

¹⁰Western ragweed.

¹¹Shrubs that tend to proliferate in response to grazing (Vesk and Westoby, 2001). Combined basal cover of roughleaf dogwood (*Cornus drummondii*), smooth sumac (*Rhus glabra*), and buckbrush (*Symphoricarpos orbiculatus*).

¹²Leadplant.

¹³New Jersey tea.

^{a, b}Within rows, means with unlike superscripts differ ($P \leq 0.05$).

growth forms, we examined basal-cover values of individual species: big bluestem, Indiangrass, and switchgrass (i.e., predominant tall growth-form grasses) and little bluestem (*Schizachyrium scoparium*) and sideoats grama (*Bouteloua curtipendula*; i.e., predominant mid growth-form grasses). These species were chosen because they

represented cumulative cover contributions of >80% of the basal cover attributed to their respective growth-form classifications across the prescribed fire regimes we evaluated. Prior to our experiment, basal cover of each of these species was not different ($P \geq 0.58$; data not shown) among treatments.

Following 4 yr of treatment, big bluestem cover was less ($P = 0.02$) in areas treated with prescribed fire in September than in areas treated with prescribed fire in either April or August (Table 2). Indiangrass basal cover was greatest ($P = 0.04$) in the August treatment and least in the September treatment; in the April treatment, it was intermediate to and not different ($P \geq 0.17$) from the August and September treatments. Basal covers of side-oats grama ($P = 0.53$) and switchgrass ($P = 0.07$) did not differ among treatments. Conversely, basal cover of little bluestem was greater ($P = 0.01$) in the September treatment than in the April or August treatment.

We concluded that the shift in basal cover between C4 tall grasses and C4 mid grasses in our experiment was primarily caused by a shift from big bluestem to little bluestem in the September fire regime. This change was not associated with treatment differences in standing forage biomass estimated via visual obstruction or nonsericea lespedeza biomass estimated via clipping (Figures 1 and 2). We further noted that C4 tall grass and C4 midgrass compositions in April and August treatments were generally similar to one another. Towne and Kemp (2008) reported that composition of C4 tall grasses was not changed when pastures were burned frequently in either April or late July to mid-August.

Basal-cover values for forbs, all growth-form classifications of forbs, and individual forb species did not differ ($P \geq 0.27$; data not shown) among treatments at the initiation of our experiment. In our final analyses of basal-cover values, total basal cover attributable to forbs also did not differ ($P = 0.16$) among prescribed-fire regimes evaluated in our experiment. There were, however, notable shifts in forb growth-form classifications among treatments (Table 2). Basal-cover values for annual forbs were greater ($P = 0.02$) in the August and September prescribed-fire treatments than in the April prescribed fire treatment; however, differences among treatments were numerically small and means were $<1.5\%$ of total basal cover. Conversely, cumulative basal-cover values of perennial forbs were less ($P = 0.02$) in the August and September treatments compared with the April treatment. To determine the nature of the change in perennial forb cover among treatments, we examined basal-cover values of sericea lespedeza, Baldwin's ironweed (*Vernonia baldwinii*), and Western ragweed (*Ambrosia psilostachya*). These were chosen because they collectively represented 77%, 50%, and 43% of final, cumulative basal cover attributable to perennial forbs in the April, August, and September fire

treatments, respectively. Additionally, we evaluated cumulative basal cover of major wildflowers because of the critical roles these plants play in food and habitat provision for invertebrate and vertebrate species native to the Kansas tallgrass prairie (Beran et al., 1999; Ogden et al., 2019).

Basal covers of sericea lespedeza, Baldwin's ironweed, and western ragweed in areas treated with fire in April were greater ($P \leq 0.01$) than in areas treated with fire in August or September (Table 2). Towne and Kemp (2008) indicated prescribed burning during summer resulted in greater variation in western ragweed cover than prescribed burning during spring, whereas frequency of Baldwin's ironweed was not different between watersheds burned in spring or summer. Effects of prescribed-fire timing on sericea lespedeza have not been widely evaluated (Cummings et al., 2007).

Sericea lespedeza, Baldwin's ironweed, and western ragweed tend to proliferate in response to grazing by large herbivores and are thought to have limited value in beef cattle diets (Stubbendieck et al., 1992; Haddock, 2005). We interpreted our results to indicate that prescribed burning of native tallgrass prairie in August or September controlled vegetative propagation of these forbs compared with prescribed burning in early April. In the specific case of sericea lespedeza, prescribed burning in early August resulted in a 54% decline in basal cover compared with prescribed burning in early April, whereas prescribed burning in early September resulted in a 76% decline in basal cover compared with prescribed burning in April (Table 2). Koger et al. (2002) reported similar control of mature sericea lespedeza plants with a foliar application of metsulfuron methyl, a commonly used pasture herbicide in Kansas. These authors noted that viable juvenile plants remained following herbicide treatments and attributed survival to the nature of aerial herbicide application above an inherently dense plant canopy. Some herbicide was likely intercepted by overstory plants and did not reach the understory occupied by sericea lespedeza seedlings. In contrast, growing-season prescribed fires in our experiment probably affected both adult and juvenile sericea lespedeza plants because such fires are generally carried by fine fuels on or near the surface of the soil.

Reductions in basal covers of sericea lespedeza, Baldwin's ironweed, and western ragweed were accompanied by a concomitant increase ($P = 0.03$) in combined basal cover of major wildflowers in the August and September treatments compared with the April treatment (Table 2). In contrast,

controlling sericea lespedeza with herbicides may result in collateral damage to sensitive nontarget forbs, such as wildflowers (Blocksome, 2006; Cummings et al., 2017; Gatson, 2018). Utilization of herbicides in native grasslands for the control of other invasive or undesirable species, including broom snakeweed (*Gutierrezia sarothrae*; McDaniel et al., 2000), leafy spurge (*Euphorbia esula*; Rinella et al., 2009), and smooth sumac (*Rhus glabra*; Tunnell et al., 2006), likewise reduced the frequency of native forbs. Native forbs are an essential food source for native invertebrates, which are in turn food sources for grassland-nesting birds (Beran et al., 1999; Ogden et al., 2019).

Before our experiment began, total basal shrub cover, combined basal cover of increaser shrubs, and basal cover of individual shrub species were not different ($P \geq 0.16$) among treatments. In our final analyses, total basal cover attributed to woody-stemmed plants was again not different ($P = 0.50$) among April, August, and September burn treatments and was generally below accepted norms for tallgrass prairie grazing systems (Table 2). Conversely, combined basal cover of increaser shrubs was less ($P = 0.04$) in August than in April and September. Basal cover of leadplant (*Amorpha canescens*), a documented component of beef cattle diets (Sproul et al., 2010; Aubel et al., 2011), was not affected ($P = 0.31$) by prescribed-fire timing, whereas New Jersey tea (*Ceanothus americanus*) basal cover was greater ($P < 0.01$) in the August treatment than in the April or September treatments. New Jersey tea has significant value as a forage resource for herbivores and as a nectar source for grassland insects (USDA-NRCS, 2010).

Plant Species Diversity

Evenness, dominance, and diversity of all plant species and native plant species only were not influenced ($P \geq 0.09$) by the timing of prescribed burning in our experiment (Table 3). In general, species evenness values were similar to those reported by Hickman et al. (2004) for annually burned tallgrass prairie managed under moderate grazing intensity. In contrast, diversity was generally greater than that reported by Randa and Yunker (2001) on restored tallgrass prairie that was either burned or mowed. Diversity of undisturbed, native tallgrass prairie remnants was reportedly greater than that of restored tallgrass prairie sites (McLachlan and Knispel, 2005; Polley et al., 2005). In our experiment, overall plant species richness and native

Table 3. Effects of the timing of annual prescribed burning on plant species diversity on native tallgrass prairie in nine fire-management units (5 ± 2.6 ha) in the Kansas Flint Hills

Item	Prescribed-burn time			SEM ¹
	April	August	September	
Overall species diversity ²				
Richness	22 ^a	27 ^b	27 ^b	1.6
Evenness	0.74	0.71	0.69	0.022
Simpson diversity	0.87	0.84	0.81	0.043
Simpson dominance	0.42	0.46	0.47	0.033
Native species diversity ³				
Richness	21 ^a	25 ^b	26 ^b	1.6
Evenness	0.73	0.70	0.69	0.021
Simpson diversity	0.83	0.81	0.80	0.042
Simpson dominance	0.45	0.48	0.48	0.033
Graminoid diversity ⁴				
Richness	10	11	11	0.6
Evenness	0.82	0.81	0.82	0.021
Simpson diversity	0.74	0.74	0.74	0.039
Simpson dominance	0.50	0.52	0.50	0.034
Forb diversity ⁵				
Richness	10 ^a	15 ^b	15 ^b	1.2
Evenness	0.70 ^a	0.76 ^b	0.81 ^b	0.039
Simpson diversity	0.57 ^a	0.73 ^b	0.83 ^b	0.066
Simpson dominance	0.65 ^a	0.52 ^b	0.45 ^b	0.057

Burn units were assigned randomly to one of three prescribed-burn times: April (1 April \pm 10.7 d); August (1 August \pm 1.9); or September (1 September \pm 2.7 d). Treatments were applied on or near target dates from 2014 to 2017.

¹Mixed-model SEM associated with comparison of treatment main-effect means.

²Diversity measures calculated from all plant species encountered.

³Diversity measures calculated from native plant species composition only.

⁴Diversity measures calculated from grass and grass-like species composition only.

⁵Diversity measures calculated from forb species composition only.

^{a,b}Within row, means with unlike superscripts differ ($P \leq 0.05$).

plant species richness were greater ($P < 0.01$) in the August and September fire treatments than in the April fire treatment. Towne and Kemp (2008) observed similar trends in plant species richness on tallgrass prairie that was burned frequently in the summer compared to adjacent areas that burned frequently in the spring.

Richness, evenness, and dominance were not different ($P \geq 0.46$) among graminoid species in areas treated with prescribed fire in April, August, or September (Table 3). Frequency and cover attributable to 10 native tallgrass prairie graminoids was generally stable over a 14-yr period between spring and summer prescribed-fire regimes according to Towne and Kemp (2008). In contrast, forb richness, evenness, and diversity were greater ($P \leq 0.02$)

in areas treated with prescribed fire in August and September during our experiment than in areas treated with prescribed fire in April. Additionally, dominance was less ($P < 0.01$) in the August and September treatments than in the April treatment, possibly indicating more favorable balance between forb community components in the August and September treatments.

Although total basal cover of forbs did not differ ($P = 0.16$; Table 2) among treatments, there were 50% more ($P < 0.01$) forb species present in the August and September treatments than in the April treatment (Table 3). Forb evenness was greater ($P = 0.02$) also in the August and September fire treatments than in the April fire treatment. Mean basal cover of sericea lespedeza in the April treatment was 7.3% of total basal vegetation cover, more than 2× that in the August treatment and more than 4× that in the September treatment (Table 2). As sericea lespedeza was progressively weakened by growing-season prescribed fires, native forb species appeared to be able to colonize voids left by sericea lespedeza.

Although forbs are a relatively small contributor to total biomass of native tallgrass prairie, they are a key component of many ecosystem processes (Grime, 1998). Forbs are a valuable diet component for domesticated livestock, wild ungulates, birds, and invertebrates; moreover, the relative importance of forbs in the diets of herbivores changes seasonally (Cook, 1983; Aubel et al., 2011; Preedy et al., 2013; Sowers et al., 2019). Furthermore, Biondini et al. (1989) suggested that forbs were of greater diagnostic value for judging environmental conditions than other plant types; in general, greater forb heterogeneity was equated with greater overall health. Weir and Scasta (2017) reported that forb diversity and cover increased as prescribed burning was moved from spring to later times of the year. Similarly, Towne and Kemp (2008) reported linear increases in forb richness over time in areas burned during summer, whereas forb richness did not change over time in areas burned during spring.

Response by Grassland Bird and Butterfly Communities

Twenty-three bird species were identified during point-count surveys (Supplementary Appendix 4). Densities of grassland-obligate nesting songbirds, specifically grasshopper sparrow, dickcissel, and eastern meadowlark, were not negatively affected by August and September fires relative to April fires (Figure 4). Differences in densities

among treatments were not detected for dickcissel ($P = 0.70$) and eastern meadowlark ($P = 0.94$). The trend of increasing forb diversity in areas burned in August and September relative to April could be the cause of greater ($P = 0.02$) grasshopper sparrow density in August and September fire treatments when compared with April.

Although we did not observe a treatment effect on dickcissel density, our results indicated that the presence of sericea lespedeza negatively influenced nest placement. Canopy cover by sericea lespedeza at dickcissel nests was less ($P = 0.03$) than half that at paired unused points (Table 4). Previous research established that dickcissel nest placement was positively associated with greater forb and shrub cover (Frawley and Best, 1991; Jensen, 1999; Winter, 1999). Consistent with these associations, forb and shrub cover were 17% and 7% greater ($P < 0.01$), respectively, at nests compared with paired unused points (Table 4). These results indicated that the reduction in forb and shrub abundance associated with sericea lespedeza invasion decreases availability of selected nest sites for dickcissels. These results provide the first evidence that sericea lespedeza invasion is detrimental to grassland songbirds. Brooke et al. (2016) reported similar effects of sericea lespedeza on northern bobwhite (*Colinus virginianus*) nest placement.

The change in plant species composition caused by sericea lespedeza invasion may have strong effects on insect pollinators. Twenty-three butterfly species or species groups were identified across our experimental site (Supplementary Appendix 5). Grassland-specialist butterflies require certain forbs species as nectar sources or as host plants;

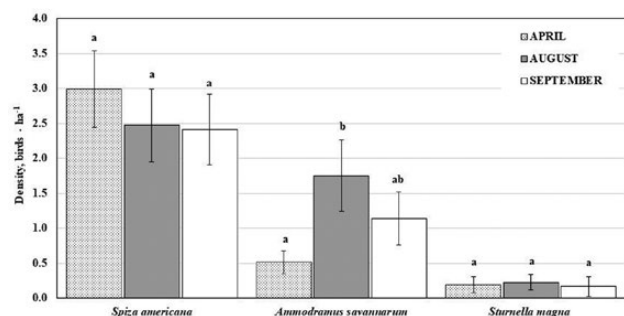


Figure 4. Densities (\pm SE) of dickcissel (*Spiza americana*), grasshopper sparrow (*Ammodramus savaannarum*), and eastern meadowlark (*Sturnella magna*) estimated from 50-m radius point-count surveys conducted between mid-May and early June 2015 and 2016. The research site was divided along natural watershed boundaries into nine fire-management units (5 ± 2.6 ha). Burn units were assigned randomly to one of three prescribed-burning times: April (1 April \pm 10.7 d); August (1 August \pm 1.9); or September (1 September \pm 2.7 d). Treatments were applied on or near target dates from 2014 to 2017. Within avian species, means with unlike superscripts differ ($P \leq 0.05$).

Table 4. Vegetation characteristics (\pm SE) measured at dickcissel (*Spiza americana*) nests and paired, unused points in annually burned native tallgrass prairie infested with sericea lespedeza (*Lespedeza cuneata*)

Item, % total cover	Nest	Unused	$F_{1,120}$	P -value
Grass	35.8 (\pm 2.31)	54.2 (\pm 3.17)	21.88	<0.01
Shrub	22.5 (\pm 3.47)	5.3 (\pm 1.46)	21.15	<0.01
Total forb	35.8 (\pm 2.89)	28.4 (\pm 2.98)	3.03	0.08
<i>Lespedeza cuneata</i>	4.9 (\pm 1.43)	12.9 (\pm 2.61)	4.88	0.03
Litter	1.7 (\pm 0.32)	3.2 (\pm 0.56)	11.09	0.01
Bare ground	2.0 (\pm 0.47)	6.4 (\pm 1.37)	3.96	0.05

Table 5. Effects of the timing of annual prescribed burning on densities (\pm SE) of the entire butterfly community and grassland-specialist butterfly species within native tallgrass prairie in nine fire-management units (5 ± 2.6 ha) in the Kansas Flint Hills

Item, density in individuals/ha	April	August	September
Complete butterfly community	12.15 (\pm 4.49) ^a	3.00 (\pm 0.88) ^b	4.81 (\pm 0.88) ^b
Grassland specialist butterfly community	0.44 (\pm 0.19) ^b	0.85 (\pm 0.39) ^a	0.89 (\pm 0.43) ^a
Shannon diversity	0.764 ^b	1.972 ^a	1.701 ^a

Burn units were assigned randomly to one of three prescribed-burning times: April (1 April \pm 10.7 d); August (1 August \pm 1.9); or September (1 September \pm 2.7 d). Treatments were applied on or near target dates from 2014 to 2017.

^{a,b}Within row, means with unlike superscripts differ ($P \leq 0.05$).

these plants become scarce when sericea lespedeza dominates the plant community. Of the three prescribed-fire treatments evaluated in our experiment, density of the butterfly community tended to be greatest ($P < 0.05$) but diversity was least ($P < 0.05$) in the April fire treatment (Table 5). In those areas, butterfly detections were dominated by eastern-tailed blues (*Cupido comyntas*), a generalist species that we observed using sericea lespedeza as a nectar source. When considering only grassland-specialist butterfly species (i.e., regal fritillary [*Speyeria idalia*], great spangled fritillary [*Speyeria cybele*], and common wood-nymph [*Cercyonis pegala*]; Vogel et al., 2007), there were no differences in densities among treatments ($P = 0.47$).

We interpreted these data to indicate that prescribed burning during August or September effectively reduced basal frequency, canopy dominance, opportunities for allelopathy, and seed-based reproductive capabilities of sericea lespedeza compared with conventional prescribed burning in April. Shifting prescribed burning from the

dormant season to the growing season was associated with diminished sericea lespedeza aerial frequency, stem length, and whole-plant dry mass at dormancy. It was also associated with lesser sericea lespedeza biomass during the final year of our experiment. Based on this evidence, we concluded that prescribed burning conducted during the growing season probably inhibited the ability of sericea lespedeza to compete with native plants. We speculated that diminished basal cover of sericea lespedeza may have been associated with greater winter-season mortality of seedlings, due to seed scarification and subsequent germination caused by prescribed fire applied during the latter portions of the growing season.

Altering the timing of prescribed burning from the traditional spring season to either August or September did not result in measurable changes to total forage biomass, bare soil, litter, total basal vegetation cover, C4 grass cover, C3 graminoid cover, or forb cover. Growing-season prescribed burning provided adequate control of woody plants when compared with prescribed burning during spring. Importantly, prescribed burning during the growing season placed selective pressure on sericea lespedeza and certain other undesirable forbs and shrubs that prescribed fire during the dormant season was unable to achieve. Additionally, growing-season prescribed fire had neutral or positive effects on native grassland bird and butterfly populations. We concluded that prescribed burning during August or September provided an inexpensive and comprehensive means to control seed-based and vegetative sericea lespedeza propagation, while improving forb diversity, improving habitat for native pollinators, and enhancing overall ecosystem health without decreasing the value of grasslands for grazing or nesting grassland birds. Further research appears warranted to investigate how best to incorporate summer-season prescribed fire into common grazing-management practices in the Kansas Flint Hills.

SUPPLEMENTARY DATA

Supplementary data are available at *Translational Animal Science* online.

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