

RESEARCH ARTICLE

Sustained management is necessary to suppress *Sericea lespedeza* (*Lespedeza cuneata*) population growth in a landscape of tallgrass prairie reconstructions

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Abstract

Introduction: *Sericea lespedeza* (*Lespedeza cuneata*) is a nitrogen-fixing legume that is native to Asia and was promoted in the central United States for forage, wildlife habitat, and to mitigate erosion and mine spoils. It has since become a high-impact invasive plant, especially in tallgrass prairie ecosystems. Traditionally, herbicide is the common tool to control *Sericea lespedeza*'s spread and manage its impact; however, herbicide treatments come at a cost to other restoration efforts.

Objectives: This research was conducted to evaluate the effectiveness of management to control *Sericea lespedeza* populations within a chronosequence of reconstructed tallgrass prairies.

Methods: We compared the difference in *Sericea lespedeza* coverage across 98 (25 m²) paired plots from 2019 to 2023 representing (1) managed and (2) management-excluded treatments along with differences in the *Sericea lespedeza* seed bank after 4 years.

Results: Findings from this study suggest that *Sericea lespedeza* populations continue to grow in the absence of management, increasing to 13 times their original densities, while populations in areas of sustained management remained stable around 2–5% coverage with year-to-year variation. Without management, the *Sericea lespedeza* soil seed bank was also five times more abundant. Older prairie reconstructions were more resistant to increases in *Sericea lespedeza* abundance but were not immune. Results also suggest that management may negatively impact forb populations, but without management both forb and graminoid populations declined.

Conclusions: This study highlights the importance of maintaining and prioritizing resources for the long-term control of aggressive invasive plants.

Implications for Practice: In prairie restorations and reconstructions, the need for frequent *Sericea lespedeza* control preempts resources that could otherwise be used for other habitat improvements. Reconstruction approaches did not have a noticeable effect on the abundance of *Sericea lespedeza*. Maintaining sustained control of *Sericea lespedeza* is important for reducing impact on plant communities and suppressing its population growth, regardless of reconstruction age. Older reconstructions were more resistant to increases in *Sericea lespedeza*, but if undetected and unmanaged, existing populations may increase. A skip year of control may be possible in prairie reconstructions that are well developed, where *Sericea lespedeza* is scarce, and where robust monitoring programs can quickly respond.

Key words: biotic resistance, competition, herbicide, plant community, seed bank, succession

Introduction

Tallgrass prairie restorations (i.e. rehabilitation of degraded prairie communities) and reconstructions (i.e. reestablishment of prairie communities on previously agricultural lands) are important for conserving biodiversity and sustaining ecosystem services, especially in the Midwestern United States where remnant prairies are extremely rare. Tallgrass prairies occupied nearly 40% of Missouri prior to Euro-American colonization, but today less than 0.1% remains because of urbanization and conversion to agriculture (Christisen 1972; Samson & Knopf 1994). Prairie reconstructions on previously agricultural lands serve as one of the few remaining options for maintaining and promoting this ecological community on the landscape (Larson et al. 2018). In addition to successful germination of seeded species and presence of conservative species (i.e. a plant community resembling that found in a high-quality remnant prairie), an important metric of success for prairie

reconstructions is dominance of native species with low abundance of invasive plants that remain in check with little maintenance (Larson et al. 2017, 2018). In practice, however, invasive plants are a major threat to prairie reconstructions, with control efforts occupying 10–90% of managers' time (Rowe 2010). The effort put toward invasive plant control defers resources

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from additional reconstruction projects, and the intensive treatments required for effective control can have deleterious impacts on native plant populations due to disturbance and non-target impacts. Thus, knowing when invasive plant populations are low enough to be maintained or moderated by the competitive interactions with native plants is important not only for assessing reconstruction success but also for shifting resources to new reconstruction efforts and other management practices (e.g. application of prescribed fire).

As invader populations move beyond feasible eradication, management transitions to suppression or containment with guidance on achieving “functional eradication” being important (Green & Grosholz 2021). Green and Grosholz (2021) define functional eradication as the point at which management suppresses invader populations to levels that reduce their unacceptable effects in high-priority ecological communities. Translating this to larger management scales, particularly with multiple small, inconspicuous populations or large disjunct or remote populations, challenges the allocation of time and financial resources and, ultimately, the successful control of invasive species (Pile Knapp et al. 2023; McMillan et al. 2023a, 2023b).

The purpose of prairie reconstruction is to successfully establish and sustain a diversity of native species that reflect their historic composition on sites that have been altered by past land uses. Reconstruction practices address the need to establish native plant species, often in conjunction with removing non-native species, and establish functional disturbances to maintain the ecosystem through time. Practices to establish the plant community during reconstruction can include row cropping with corn or soybeans for site preparation, overseeding existing vegetation, or drilling often in combination with herbicide to reduce the abundance of non-native plants. Fire, grazing, or their combination (called pyric herbivory) is commonly used to facilitate late-successional species composition and sustain the native prairie plant community through time (Fuhlendorf et al. 2009; Applestein et al. 2018; Newbold et al. 2020).

Succession of prairie communities has been characterized as a continuous process marked by developmental stages of plant dominance (Schramm 1990; Betz et al. 1996). Reconstruction of late-successional prairie communities (i.e. the continued development of mature, late-climax species such as Lead plant [*Amorpha canescens*] and Prairie dropseed [*Sporobolus heterolepis*] with a concomitant reduction in early successional species identified by Schramm 1990) may help reduce invasion risk through competition and establishment limitation (Blumenthal et al. 2003, 2005). Young reconstructions, which are initially dominated by prairie annuals and large grasses (Schramm 1990; Betz et al. 1996), can be plagued by invasive plants that may persist as the community ages (Larson et al. 2017). Research suggests that targeted control efforts, such as herbicide application, can be effective at the plot or site scale when invasive plant populations are abundant, although these treatments may have unintended non-target impacts on communities (Pile Knapp et al. 2023). For example, the control of invasive grasses intended to facilitate the growth and nectar production of native forbs using a grass-specific herbicide led to increases in other invasive plants, reducing the potential benefits for an endangered butterfly (Bennion et al. 2020).

Although invasive plant control is often assessed by impacts on aboveground biomass, managing the seed bank is also important for successful long-term control of plant invaders (Robertson & Hickman 2012). Reducing the abundance of the invader aboveground may not necessarily lead to reductions in the residual invasive seed bank. Understanding how management influences seed bank composition may help to determine plant community response to disturbance events, including fire, because invasive plants in the seed bank often benefit from disturbance (McNicoll & Augspurger 2010). In a prairie restoration study in the northern Great Plains, clipping, herbicide, or enrichment seeding did not affect the seed bank of Crested wheatgrass (*Agropyron cristatum*), despite increasing native species cover and richness aboveground (Wilson & Pärtel 2003). Furthering our knowledge on the interactions of non-target impacts and residual invasive seed bank following invasive plant control efforts will aid management prescriptions in active prairie reconstructions that are challenged by invasive plants.

One such challenging invasive plant in the central United States is *Sericea lespedeza* (*Lespedeza cuneata* [Dum. Cours.] G. Don). *Sericea lespedeza* is a non-native, invasive legume of Asian origin that commonly invades disturbed habitats, including open fields and pastures, and threatens tallgrass prairies (Eddy & Moore 1998; Silliman & Maccarone 2005). Traits that contribute to its invasive potential include a tall, branched stem architecture with widely branched and deep roots (Brandon et al. 2004; Allred et al. 2010), abundant seed production (Woods et al. 2009), allelopathy that limits the growth and establishment of other plants (Kalburtji & Mosjidis 1993), and the ability to alter soils to favor its own growth (Coykendall & Houseman 2014). Additionally, *Sericea lespedeza* is known to produce a persistent seed bank, the longevity of which is not well understood (Gucker 2010). Herbicides can be effective at controlling *Sericea lespedeza* (Altom et al. 1992), but herbicide efficacy may diminish as the growing season progresses (Farris & Murray 2009) and at larger spatial scales because thorough, repeated application of herbicide is often impractical at large scales (McMillan et al. 2023a).

This project was designed to address specific challenges associated with controlling *Sericea lespedeza* across a large managed landscape of prairie reconstructions of varying ages. Previous research from the study location compared plant community responses in reconstructions to reference tallgrass prairies, reporting older reconstructions better approximated reference communities than newer reconstructions (Newbold et al. 2020). The study location has been managed operationally. The default management action was to annually spot treat *Sericea lespedeza* with herbicide, which we used as a baseline to compare to population changes over time following cessation of annual herbicide control. Specifically, we addressed several questions: (1) Does the initial prairie reconstruction approach (i.e. row cropping vs. seeding only) influence *Sericea lespedeza* populations? (2) Are older prairie reconstructions less invaded than younger prairie reconstructions, providing evidence that later-successional communities are more resistant to invasion? (3) How does management, applied across the landscape, influence *sericea* populations? (4) How does the plant community

respond to management versus no management of *Sericea lespedeza*? (5) How does the *Sericea lespedeza* seed bank respond to sustained herbicide control? These questions aim to address the following management conundrum: *If true eradication is highly unlikely, when are invasive plant populations low enough to accept “functional eradication” (sensu Green & Grosholz 2021) and thereby reduce management effort?*

Methods

Site Description

Our study site was located at Prairie Fork Conservation Area (PFCA), a 369 ha mosaic of prairie, savanna, and woodland natural communities. These communities differ in tree cover and species assemblages due to interactions between edaphic conditions and disturbance (i.e. fire) (Nelson 2005). To date, considerable progress has been made in the reconstruction of prairie communities at PFCA (Newbold et al. 2020), but eradicating *Sericea lespedeza* has remained challenging. In the 1990s, *Sericea lespedeza* was widespread and dominant across the property. Prairie reconstruction efforts began at PFCA in 2004, and based on data collected in 2017, *Sericea lespedeza* populations averaged across all reconstructions, regardless of age, had been managed to less than 2% of total plant cover (C. Newbold, unpublished data). This degree of success spurred conversations from managers and decision-makers about whether continued control treatments at the same scale and effort were warranted or if treatments could be lessened in frequency, which served as the impetus for this project.

Prairie reconstruction at PFCA uses either herbicide-resistant cropping or overseeding for initial establishment of native plant species, followed by prescribed burning, haying, and annual *Sericea lespedeza* herbicide applications for maintenance (Newbold et al. 2020). Round-up ready cropping removes existing vegetation to prepare the seedbed for planting by using commercial farming practices. Although it is the preferred practice by prairie restoration practitioners, this method is not always feasible, so other methods of site preparation, such as broadcast herbicide application with overseeding are used (Rowe 2010; Newbold et al. 2020). Prior research at PFCA suggests that these practices can differ in the time it takes for the establishment of native plants, which may influence *Sericea lespedeza* populations (Study Question 1) (Newbold et al. 2020).

After initial reconstruction treatments, regular maintenance treatments included prescribed burning and haying. Both treatments are intended to reduce the competitiveness of grasses and improve the establishment and growth of forbs, in addition to managing woody encroachment and invasive plants (Rowe 2010). Managers on PFCA adjust annual prescriptions based on their knowledge and experience. Haying is used in rotation with prescribed fire, particularly when growing season burns are limited by weather or fuel conditions. Haying is also used to supplement local farmers during drought years when hay is scarce. Haying is conducted after July 15 to minimize impacts to ground nesting birds but prior to *Sericea lespedeza* seed set. Haying is also suspected to make herbicide

applications more effective because the regrowth of *Sericea lespedeza* is more identifiable following haying. Herbicide is applied as foliar spot sprays targeted at *Sericea lespedeza* using backpack- or utility terrain vehicle-mounted sprayers with PastureGard (Corteva Agriscience, Riverside, CA, U.S.A.; Triclopyr [45.07%] and Fluroxypyr [15.56%], active ingredients), which is a broadleaf herbicide, used according to product labeling with ammonium sulfate as a surfactant. All areas classified for reconstruction as a prairie natural community across PFCA are prioritized by the management staff for herbicide and/or haying treatment twice during the growing season, once in June–July and then again in July–August. When *Sericea lespedeza* population sizes are large, tractor-mounted broadcast applications are applied with Escort (Bayer Environmental Science, Canada; Metsulfuron methyl [60%], active ingredient) when *Sericea lespedeza* is flowering.

Field Study

To evaluate both the influence of reconstruction age (Study Question 2) and the effectiveness of current control methods on *Sericea lespedeza* populations (Study Question 3), we established 49 pairs of 25 m² plots across 21 reconstructed prairie units at PFCA (98 total; Fig. 1). These plots were established prior to the 2019 growing season, across a range of reconstruction age classes, that include “new” (age 0–3 years since initial planting), “young” (age 4–7 years since initial planting), and “established” (age 8+ years since initial planting) reconstructions regardless of their reconstruction origin (i.e. cropping vs. herbicide and overseeding). New reconstructions were comprised of species such as Pinnate prairie coneflower (*Ratibida pinnata* [Vent.] Barnhart), Canada wildrye [*Elymus canadensis* L.], Annual ragweed [*Ambrosia artemisiifolia* L.] along with non-native grasses such as Yellow foxtail (*Setaria glauca* [Poir.] Roem. & Schult. spp. pumila) and Tall fescue (*Festuca arundinaceus* [Schreb.]. Young reconstructions were comprised of species such as Big bluestem (*Andropogon gerardii* Vitman), White wild indigo (*Baptisia alba* [L.] Vent.), Wholeleaf rosinweed (*Silphium integrifolium* Michx.), bearded beggarticks (*Bidens aristosa* [Michx.] Britton), and Baldwin’s ironweed (*Veronica baldwinii* Torr.). Established reconstructions were comprised of species such as Button eryngo (*Eryngium yuccifolium* Michx.), Ashy sunflower (*Helianthus mollis* Lam.), Willowleaf aster (*Symphotrichum praealtum* [Poir.] G.L. Nesom), Blue wild indigo (*B. australis* [L.] R. Br.), and Prairie dropseed (*Sporobolus heterolepis* [A. Gray] A. Gray). Prior research indicated that reconstruction age and establishment method were influential for plant communities at PFCA; however, with time, plant communities in mature reconstructions began to approach those of nearby remnant prairies, based on coefficients of conservatism and Floristic Quality Index (Newbold et al. 2020). Plot locations were determined by establishing a 50 × 100 m grid overlay in ArcGIS and positioning paired plots at each grid point within the prairie natural community type designation. Of the plots, 76 were reconstructed using round-up ready cropping and 22 by overseeding.

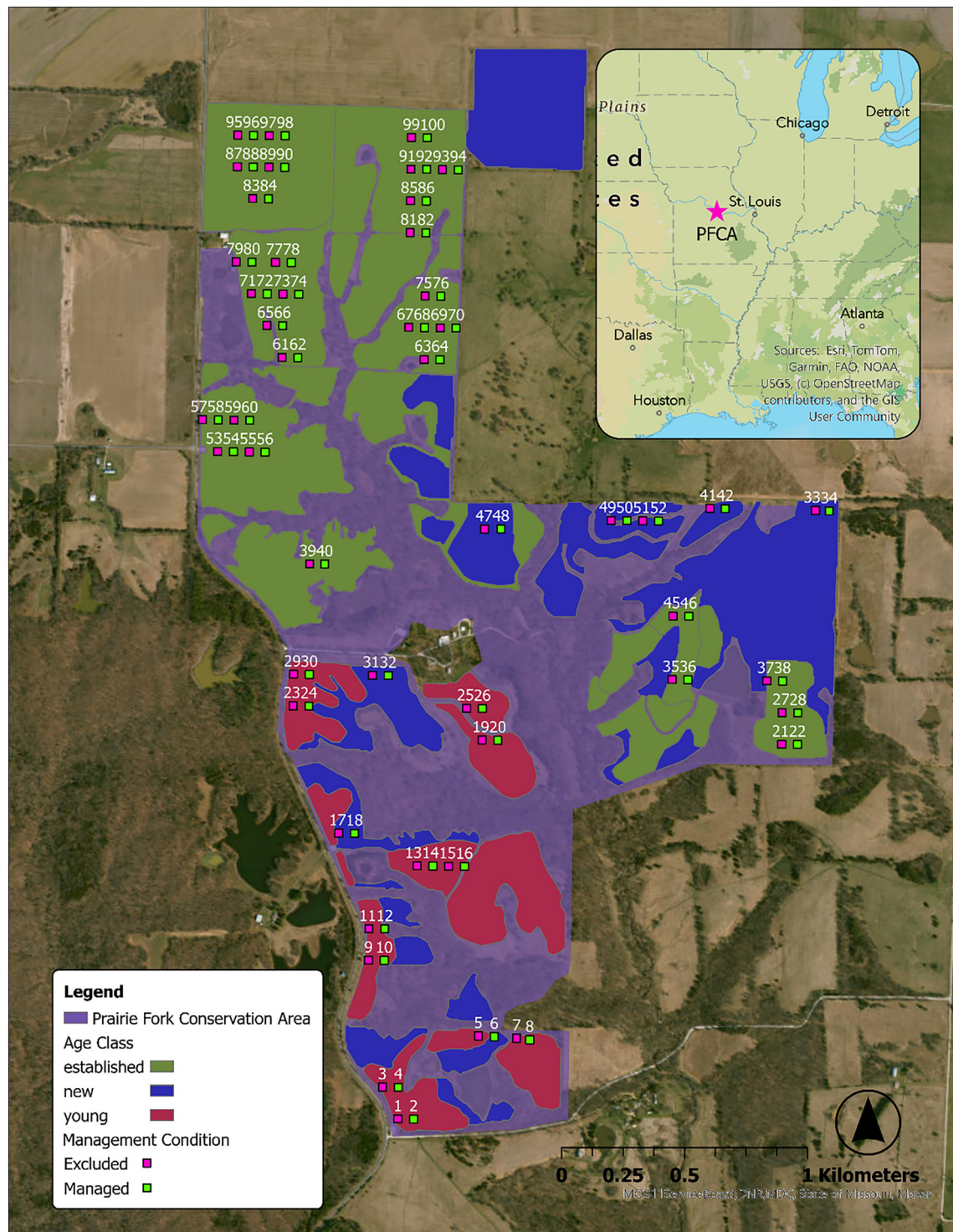


Figure 1. Map of *Sericea lespedeza* paired management conditions (managed vs. excluded) plot locations by reconstruction age class at Prairie Fork Conservation Area (PFCA) located in Callaway County, Missouri.

In each treatment pair, one plot represented “management as usual,” and the paired plot served as “management excluded” (i.e. untreated). Hereafter, we refer to these two management conditions as “managed” and “excluded,” respectively. The

excluded plots were removed from *Sericea lespedeza* herbicide applications and haying beginning in 2019. Excluded plots were made conspicuous by flagging 1.2 m t-posts in each of the four plot corners. Managed plots were made inconspicuous by using

buried 1.9 cm diameter conduit for plot corners, which were re-located using a metal detector, and treated operationally to represent business-as-usual PFCA management. Whether a particular managed plot was treated depended on an individual reconstruction being prioritized for *Sericea lespedeza* control and whether stems of *Sericea lespedeza* were present and detected by the herbicide applicator. Generally, all reconstructions were treated at least annually, except for 2020 when staffing was restricted due to coronavirus disease 2019. We did not direct control efforts to specific locations or plots because we wanted to capture typical adaptive management approaches used at PFCA (Study Question 3). Unfortunately, two inconspicuous managed plots, one each in the new and established reconstructions, were unable to be located after the first year of the study and were subsequently removed. However, we continued to monitor their paired plots, where management was excluded.

Within each plot, we assessed the effect of removing management on *Sericea lespedeza* populations (Study Question 3) and the response of the plant community including native and non-native species (Study Question 4) by recording coverage of functional groups (i.e. forbs, graminoids, shrubs, subshrubs, trees, and vines) and *Sericea lespedeza* using a modified Daubenmire scale (0–1%, 1–5%, 5–10%, 10–25%, 25–50%, 50–75%, 75–95%, and 95–100%) (Abrams & Hulbert 1987) across the entirety of each 25 m² plot. Coverages by functional group were independent of other functional groups allowing for the potential of total plant coverage to be greater than 100%. Additionally, we downscaled our monitoring to improve *Sericea lespedeza* cover estimates by establishing four 1 m² sub-plots offset diagonally 1 m from each plot corner. To determine plot-level abundances of *Sericea lespedeza* for analysis we calculated average coverage of the four quadrats. Annual sampling occurred in July–August from 2019 to 2023.

Seed Bank Study

In late January 2023, 4 years following the initiation of the study, we evaluated the soil seed bank of each plot (Study Question 5). January was selected for sampling to facilitate easier soil collection in the dormant season, sample the seedbank after seed set, and allow for chilling to occur. We assessed the presence and abundance of *Sericea lespedeza* seed in the soil by initiating germination under greenhouse conditions. We extracted five soil cores (203 cm³; 5 cm *H* × 7.23 cm *W*; 0.08% of the total plot area) from the soil surface of each plot with a ProPlugger (<https://proplugger.com/>, Waxhaw, NC, U.S.A.). Four samples were taken 1 m from the middle (2.5 m) of each plot edge (each plot edge was 5 m in length) and one sample from the plot center. The samples were aggregated to the plot level in paper bags and taken to the University of Missouri, Ashland Road Greenhouse. The aggregated samples were spread across plant flats (27.8 cm *W* × 54.5 cm *L* × 6.2 cm *D*) and filled with Promix potting soil within several days of collection. Samples remained in protected, outside ambient conditions during that time, which were at or below freezing prior to planting. The depth of the field soil was approximately 2 cm with potting soil approximately

4 cm in depth. The flats were grown under ambient (i.e. not heated, evaporatively cooled, no supplemental lighting) greenhouse conditions with watering occurring two to three times a week to facilitate the germination of *Sericea lespedeza* seedlings as needed until May 2023, at which time we determined that new germinations had ceased. Temperatures in the greenhouse did not go below 4.5°C or exceed 26.7°C during the study period. Diurnal temperature fluctuations were not recorded. Trays were rotated around the greenhouse every 2 weeks. The trays were monitored weekly for germination of *Sericea lespedeza* seedlings. All seedlings were counted, recorded, and removed during each visit.

Data Analyses

To determine if the initial reconstruction practice (i.e. round-up ready cropping or overseeding) influenced *Sericea lespedeza* abundance or presence at the start of the study (Study Question 1), we used generalized linear mixed models to assess differences in coverage and presence of *Sericea lespedeza* in 2019. The presence of *Sericea lespedeza* was modeled using a logistic regression framework, using a binomial distribution with a logit link function. To assess management effectiveness in controlling *Sericea lespedeza* populations across prairie reconstruction ages (Study Questions 2 and 3), we developed a repeated measures GLIMMIX model in SAS (version 9.4, SAS Institute Inc., Cary, NC, U.S.A.) with an autoregressive covariance structure that evaluated the combined plot-level mean coverage of *Sericea lespedeza* by management condition (i.e. managed or excluded), reconstruction age class (i.e. new, young, or established), year, and their interactions using a lognormal distribution. To assess the change in *Sericea lespedeza* populations from 2019 to 2023, we calculated the change in coverage for each plot as the difference in abundance between the two time periods (i.e. 2023 minus 2019). We developed a model with management condition, reconstruction age class, and their interaction as fixed effects using a lognormal distribution. To deal with negative values, 100 was added across the dataset, but data are reported in their original form. Further, to assess the influence of *Sericea lespedeza* presence at the beginning of the study on the change in *Sericea lespedeza* abundance after five growing seasons, we ran the same model but included a term for presence/absence of *Sericea lespedeza* in 2019.

To determine how the plant community responded to *Sericea lespedeza* control (Study Question 4), we examined changes in the two dominant functional groups, forbs and graminoids, using the same model used to assess change in *Sericea lespedeza* populations. The other functional groups (i.e. shrubs, subshrubs, trees, and vines) occurred too infrequently for formal analysis. Additionally, to assess the relationship between change in *Sericea lespedeza* abundance by management condition as it related to initial forb and graminoid abundance and change in forb and graminoid abundance over time, we developed linear regression models with change in *Sericea lespedeza* coverage as the dependent variable. We also assessed the linear relationships by reconstruction age class.

To assess the effect of management on the *Sericea lespedeza* seed bank (Study Question 5), we modeled the number of *Sericea lespedeza* seedlings that germinated under greenhouse

conditions by treatment and reconstruction age class using a negative binomial hurdle model to account for the zero-inflated dataset and assessed overdispersion and goodness-of-fit with the Pearson statistic.

For all analyses, significance was determined at an α of 0.05. Analyses were performed in SAS 9.4 (SAS Institute Inc., Cary, NC, U.S.A.). Data are reported in their original form using means and standard error of the mean.

Results

Overarching Model Results

Sericea lespedeza, forb, and graminoid populations were similar across prairie reconstruction age classes and treatment type (i.e. managed vs. excluded) in 2019 (Table 1). *Sericea lespedeza* populations ranged from 0.6 to 2.4% coverage in new and young reconstruction age classes and less than 1% coverage in established reconstructions. Forb abundance ranged from 48 to 62% coverage and graminoids ranged from 33 to 55% coverage across reconstruction age classes. New and young reconstructions had greater variability in their populations of forbs and graminoids than established reconstructions. At the start of the study, *Sericea lespedeza* was present in 31 plots (17 management plots and 14 management-excluded plots). Four years later, *Sericea lespedeza* presence doubled, with detections in 61 plots (31 managed and 30 excluded). Generally, the results of our models suggest that the actual coverage of *Sericea lespedeza* was affected by management condition ($F = 5.9$; $p = 0.0184$), reconstruction age class ($F = 6.9$; $p = 0.0014$), year ($F = 8.3$; $p < 0.001$), and the interactive effects of condition by year ($F = 5.1$; $p = 0.0008$) and reconstruction age class by year ($F = 3.0$; $p = 0.0039$; Table S1). In contrast, when we modeled the change in the *Sericea lespedeza* populations, reconstruction age class was not important ($F = 0.8$; $p = 0.4179$) but management condition was ($F = 21.2$; $p < 0.001$). Where *Sericea lespedeza* was managed, there was an average of a $2.2 \pm 1.3\%$ gain in coverage; when management was excluded, coverage of *Sericea lespedeza* grew by $12.3 \pm 2.9\%$. Further, the initial presence of *Sericea lespedeza* was important for population growth depending on reconstruction age class and condition ($F = 3.2$; $p = 0.0445$).

Study Question 1

Does prairie reconstruction practice influence Sericea lespedeza populations? The method of prairie reconstruction, either row cropping or seeding only, did not significantly influence

Sericea lespedeza coverage ($p = 0.648$) or presence ($\chi^2 = 0.312$) in 2019, when the study was initiated.

Study Question 2

Are older prairie reconstructions less invaded than younger prairie reconstructions, providing evidence that later-successional communities are more resistant to invasion? Generally, older, established reconstructions were less invaded by *Sericea lespedeza* than young reconstructions and had smaller increases in abundance when management was excluded (Table S2). The abundance of *Sericea lespedeza* was significantly higher in young reconstructions than in established ones, with new reconstructions having intermediate abundance (Table S2, Fig. 2A). Although the abundance of *Sericea lespedeza* significantly increased in all reconstruction age classes with time (Fig. 2C), young reconstructions increased the most, while established reconstructions increased the least (Fig. 2E). Established reconstructions increased an average of $5.0 \pm 0.1\%$ in coverage, followed by new ($9.2 \pm 0.8\%$) and young reconstructions ($10.5 \pm 2.2\%$). Increases were greatest when management was excluded (Fig. 2D), especially for young reconstructions.

When calculated as the change in abundance from the start to end of the study, young reconstructions also experienced the greatest increase in *Sericea lespedeza* in the absence of management (Fig. 3B). In contrast, there were numerical but not statistically significant increases in abundance when management was excluded in the new and established reconstructions (Fig. 3B). Importantly, the greatest increases in *Sericea lespedeza* for established reconstructions occurred when *Sericea lespedeza* was present at the beginning of the study period, regardless of subsequent management (Fig. 4).

Study Question 3

How does management, applied across the landscape, influence Sericea lespedeza populations? Managing *Sericea lespedeza* populations across the landscape was important for maintaining populations at low levels, especially in areas where *Sericea lespedeza* was initially present. Overall, managed plots had significantly less *Sericea lespedeza*, averaging $2.2 \pm 6.6\%$ coverage, whereas excluded plots had over twice as much, averaging $5.4 \pm 12.8\%$ coverage (Fig. 2B). As the study progressed, *Sericea lespedeza* coverage increased, with significant increases after two growing seasons since the initiation of the study (Fig. 2C). These increases were significant in excluded plots with gains in coverage occurring each year (Fig. 2D).

Table 1. Total number of plots and mean (and standard error) coverage (%) of *Sericea lespedeza*, forbs, and graminoids by prairie reconstruction age class and management condition when the study was initiated in 2019.

Age class	Condition	n plots	<i>Sericea</i> (%)	Forb (%)	Graminoid (%)
New (0–3 years)	Managed	7	1.2 (0.7)	56.0 (10.6)	32.5 (11.4)
	Excluded	8	2.4 (1.5)	48.2 (5.1)	55.4 (8.5)
Young (4–7 years)	Managed	12	2.4 (0.8)	47.9 (6.8)	50.2 (6.2)
	Excluded	12	0.6 (0.2)	62.1 (5.8)	37.5 (7.0)
Established (8+ years)	Managed	29	0.2 (0.1)	50.4 (4.3)	49.2 (4.3)
	Excluded	30	0.4 (0.3)	58.4 (3.4)	46.1 (3.7)

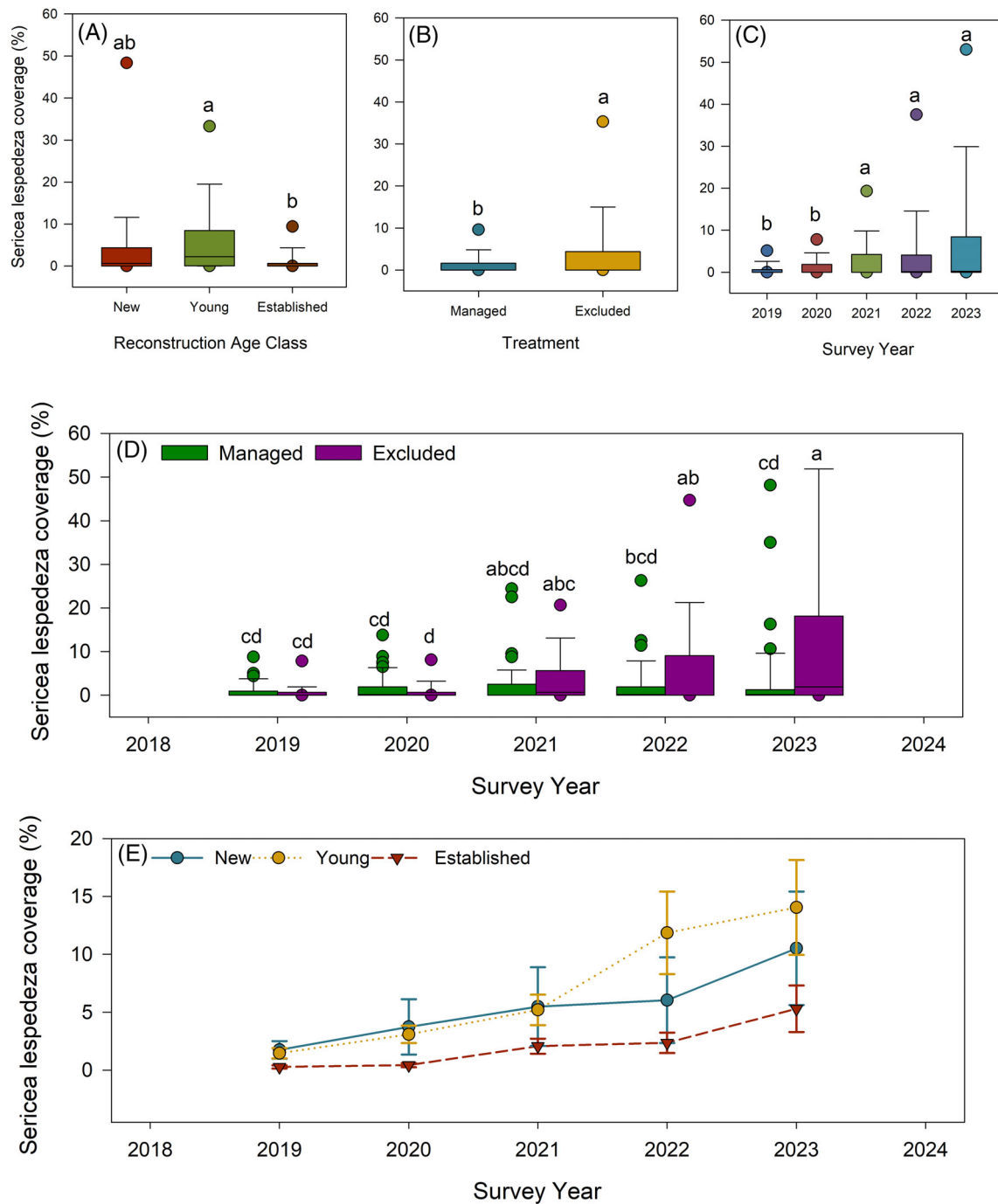


Figure 2. Relationships between *Sericea lespedeza* coverage and reconstruction age class (panel A), management condition (panel B), survey year (panel C), condition by survey year (panel D), and reconstruction age class by survey year (panel E). Significant differences between model parameters are indicated by different lower-case letters at an α level of less than 0.05. Whiskers and points represent the 5 and 95th percentiles.

Excluding management of *Sericea lespedeza*, even when populations were low, resulted in substantial increases in abundance. Over the 5-year study period, excluding management resulted in more than double the *Sericea lespedeza* abundance compared to areas where management was sustained ($5.4 \pm 12.8\%$ cover compared to $2.2 \pm 6.6\%$ cover, respectively; Fig. 2B).

When calculated as the change in abundance from the start to end of the study, populations of *Sericea lespedeza* where management was removed increased six times as much as those where management was sustained ($12.3 \pm 2.9\%$ compared to $2.2 \pm 1.3\%$, respectively; Fig. 3A), although both managed and excluded populations increased over the 5-year study period. Significant increases in *Sericea lespedeza* abundance in the absence of management occurred

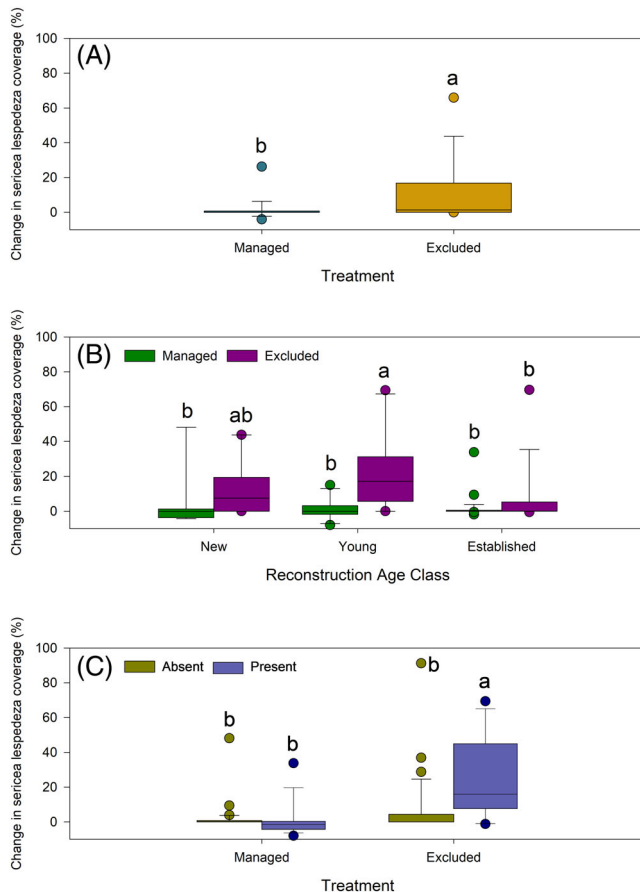


Figure 3. Relationships between the change in *Sericea lespedeza* populations from 2019 to 2023 by management condition (panel A), management condition by reconstruction age class (panel B), and management condition when *Sericea lespedeza* was present or not in the plot when the study began (panel C). Significant differences between model parameters are indicated by different lower-case letters at an α of less than 0.05. Whiskers and points represent the 5 and 95th percentiles.

in plots where the species was initially present ($F = 12.7$; $p < 0.001$; Fig. 3C). In plots where *Sericea lespedeza* was absent at the beginning of the study, its coverage increased to an average of $2.3 \pm 1.6\%$ in managed plots and $7.0 \pm 2.9\%$ in management-excluded plots, changes that were not statistically significant. In contrast, when *Sericea lespedeza* was initially present, its abundance increased by only $2.0 \pm 2.5\%$ in managed plots compared to $25.5 \pm 6.1\%$ in excluded plots. In new and young reconstructions, management was most effective at reducing or minimizing population increases when *Sericea lespedeza* was present at the start of the study and less effective when it was initially absent (Fig. 4A). The effect of excluding management was greatest when *Sericea lespedeza* was initially present, regardless of reconstruction age class, ranging from 15 to 35% increases in coverage (Fig. 4B).

Study Question 4

How does the plant community respond to management versus no management of Sericea lespedeza? Changes in prairie plant communities during the study period were primarily related to

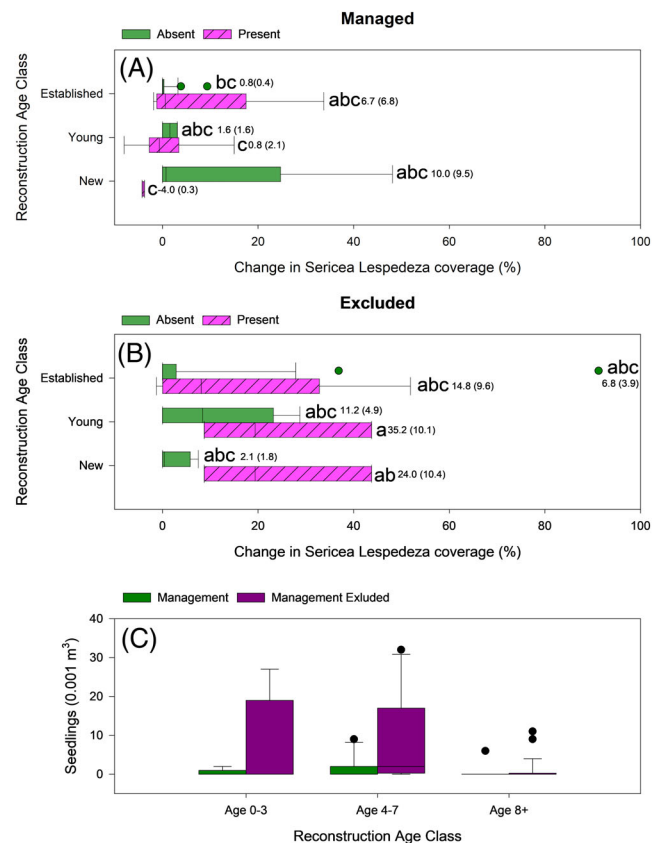


Figure 4. The change in *Sericea lespedeza* abundance during the 5-year study period by reconstruction age class, management condition (managed = panel A; excluded = panel B), and whether *Sericea lespedeza* was present or absent in the plot in 2019. Mean ($\pm$ SE) are reported on the right side of the box plot. Panel (C) is a boxplot representing the number of *Sericea lespedeza* seedlings per 0.001 m³ that grew from the soil seed bank under greenhouse conditions after 4 years of management or management exclusion by prairie restoration age class. Negative binomial model results indicated a significant difference between management condition ($p = 0.0256$) and between restoration age classes ($p = 0.0475$ and $p = 0.0089$). The interaction of management condition and restoration age class was non-significant. Significant differences between model effects are indicated by different lower-case letters at an α of less than 0.05.

changes in forb abundance in different reconstruction ages ($F = 4.3$; $p = 0.0161$). Forb abundance increased in new reconstructions ($9.5 \pm 11.7\%$) but decreased in young ($-29.2 \pm 7.0\%$) and established reconstructions ($-17.2 \pm 4.0\%$). The reductions in the forb community for young and established reconstructions were not statistically different from each other. Reconstruction age was not important for changes to the graminoid communities ($F = 2.9$; $p = 0.0586$). The interaction of management condition and reconstruction age class was not significant for the changes in forb ($F = 0.4$; $p = 0.6690$) or graminoid populations ($F = 2.4$; $p = 0.1009$).

Management condition strongly influenced changes in forb and graminoid abundances. *Sericea lespedeza* management was associated with a reduction of $-23.5 \pm 5.2\%$ in forb abundance compared to excluded plots where forbs were reduced $-8.7 \pm 4.8\%$ ($F = 4.6$; $p = 0.0347$). When *Sericea lespedeza* was managed, the reduction in forbs did not result in gains in

Table 2. Linear models for the effect of initial forb and graminoid coverage, and the change of forb and graminoid coverage on the change in *Sericea lespedeza* abundance by management condition. Linear models and test statistics in **bold** are significant at an α of 0.05. Abbreviation: RMSW, root mean square error.

Factor	Management condition	Linear model	RMSE	r ²	F stat	p Value
Initial forb coverage	Managed	$y = 1.04 + 0.02 \times \text{forb}$	9.09	0.00	0.15	0.70
	Excluded	$y = 20.41 - 0.14 \times \text{forb}$	20.58	0.02	0.75	0.39
Initial graminoid coverage	Managed	$y = 4.41 - 0.05 \times \text{graminoid}$	9.02	0.02	0.82	0.37
	Excluded	$y = -0.08 + 0.27 \times \text{graminoid}$	19.86	0.84	4.29	0.04
Change in forb coverage	Managed	$y = 1.74 - 0.02 \times \Delta \text{forb}$	9.08	0.01	0.26	0.61
	Excluded	$y = 10.12 - 0.25 \times \Delta \text{forb}$	18.93	0.17	9.48	0.00
Change in graminoid coverage	Managed	$y = 2.3 - 0.01 \times \Delta \text{graminoid}$	9.10	0.00	0.03	0.86
	Excluded	$y = 10.75 - 0.27 \times \Delta \text{graminoid}$	18.8	0.18	10.24	0.00

Sericea lespedeza abundance. However, when management was excluded, increased abundance of *Sericea lespedeza* was associated with declines in other forb abundance (Table 2; Fig. S1), especially in young reconstructions (Table 3; Fig. S2). *Sericea lespedeza* management was associated with increased graminoid coverage ($13.5 \pm 6.6\%$; $F = 12.0$; $p = 0.0008$), but when management was excluded, graminoid populations declined ($-14.5 \pm 5.0\%$). Greater initial abundance of graminoids when management was excluded was associated with smaller increases in *Sericea lespedeza* abundance (Table 2; Fig. S1B). Similar changes in forb populations, without management, increases in *Sericea lespedeza* abundance were associated with declines in graminoids, especially in established reconstructions (Table 4; Fig. S3).

Study Question 5

What is the relationship of the Sericea lespedeza soil seed bank to sustained versus excluded management? The *Sericea lespedeza* seed bank was significantly affected by management condition and reconstruction age class (Fig. 4C). Managed plots had an average of 0.6 ± 0.3 seedlings/0.001 m³, whereas excluded plots had an average of 3.8 ± 1.1 seedlings/0.001 m³

(z value = -2.2 ; $p = 0.0256$). New and young reconstructions were associated with an increased *Sericea lespedeza* seed bank relative to established reconstructions. New reconstructions had 1.9 ± 1.0 more seedlings/0.001 m³ ($z = 2.0$; $p = 0.0475$) and young reconstructions had 2.1 ± 0.8 more seedlings/0.001 m³ ($z = 2.6$; $p = 0.0089$) than established reconstructions. Similar to the field data, *Sericea lespedeza* seedling density from the seed bank was greatest in young reconstructions (5.2 ± 1.9 seedlings/0.001 m³), followed by new reconstructions (3.9 ± 2.2 seedlings/0.001 m³), with established reconstructions having fewer than 1 seedling per 0.001 m³ (0.6 ± 0.3 seedlings/0.001 m³).

Discussion

Invasive plants can have deleterious impacts on native plant communities and strain resources needed to manage them, thereby reducing resources available for conservation, restoration, and maintenance of communities across the landscape. Functional eradication is a management framework designed to suppress invasive species populations at low enough levels to reduce their ecological impacts in high-priority areas, with the understanding that complete eradication is often not operationally feasible (Green &

Table 3. Linear models for the effect of initial forb coverage, and the change of forb coverage on the change in *Sericea lespedeza* abundance by management condition and age class. Linear models and test statistics in **bold** are significant at an α of 0.05. Abbreviation: RMSW, root mean square error.

Age class	Condition	Linear model	RMSE	r ²	F stat	p Value
Initial forb coverage	New Managed	$y = 8.33 - 0.04 \times \text{forb}$	20.45	0.00	0.01	0.91
	New Excluded	$y = -8.98 + 0.42 \times \text{forb}$	16.21	0.13	0.73	0.43
	Young Managed	$y = 4.2 - 0.07 \times \text{forb}$	5.98	0.01	0.58	0.47
	Young Excluded	$y = 20.56 + 0.04 \times \text{forb}$	23.53	0.00	0.01	0.91
	Established Managed	$y = -0.70 + 0.05 \times \text{forb}$	6.46	0.03	0.88	0.36
	Established Excluded	$y = 28.41 - 0.35 \times \text{forb}$	18.94	0.11	3.35	0.08
Change in forb coverage	New Managed	$y = 5.37 - 0.06 \times \Delta \text{forb}$	20.12	0.04	0.18	0.69
	New Excluded	$y = 32.56 - 0.72 \times \Delta \text{forb}$	12.69	0.47	4.34	0.09
	Young Managed	$y = 2.81 + 0.05 \times \Delta \text{forb}$	5.88	0.09	0.88	0.37
	Young Excluded	$y = 13.15 - 0.42 \times \Delta \text{forb}$	17.59	0.44	7.91	0.02
	Established Managed	$y = 0.88 - 0.04 \times \Delta \text{forb}$	6.45	0.04	0.97	0.34
	Established Excluded	$y = 5.95 - 0.19 \times \Delta \text{forb}$	19.18	0.08	2.55	0.12

Table 4. Linear models for the effect of initial graminoid coverage, and the change of graminoid coverage on the change in *Sericea lespedeza* abundance by management condition and reconstruction age class. Linear models and test statistics in bold are significant at an α of 0.05. Abbreviation: RMSW, root mean square error.

Age class	Treatment	Linear model	RMSE	r ²	F stat	p Value
Initial graminoid coverage						
New	Managed	$y = 8.10 - 0.07 \times \text{graminoid}$	20.31	0.02	0.08	0.79
New	Excluded	$y = -12.99 + 0.44 \times \text{graminoid}$	13.53	0.39	3.23	0.13
Young	Managed	$y = -2.33 + 0.07 \times \text{graminoid}$	5.97	0.06	0.60	0.46
Young	Excluded	$y = 11.98 + 0.30 \times \text{graminoid}$	22.30	0.10	1.15	0.31
Established	Managed	$y = 4.03 + 0.05 \times \text{graminoid}$	6.48	0.03	0.76	0.39
Established	Excluded	$y = -8.00 \text{ to } 0.35 \times \text{graminoid}$	18.71	0.13	4.12	0.05
Change in graminoid coverage						
New	Managed	$y = 5.93 + 0.01 \times \Delta \text{graminoid}$	20.47	0.00	0.00	0.96
New	Excluded	$y = -7.89 \text{ to } 0.53 \times \Delta \text{graminoid}$	11.80	0.54	5.81	0.06
Young	Managed	$y = 1.31 + 0.02 \times \Delta \text{graminoid}$	6.11	0.02	0.17	0.69
Young	Excluded	$y = 23.0 - 0.23 \times \Delta \text{graminoid}$	21.94	0.13	1.52	0.25
Established	Managed	$y = 1.83 - 0.01 \times \Delta \text{graminoid}$	6.56	0.00	0.01	0.91
Established	Excluded	$y = 7.89 - 0.34 \times \Delta \text{graminoid}$	17.05	0.28	10.69	0.00

Grosholz 2021). Prairie reconstructions are inherently high-priority areas to reduce invader impacts because prairies are rare and important for meeting biodiversity needs and because reconstructions are resource-intensive to establish and maintain. Few studies assess functional eradication in an operational landscape that has meaningful implications for land managers, a knowledge gap that our study seeks to fill. Our work suggests that (1) different initial prairie reconstruction practices can be equally effective in subsequent control of invasive plant populations, (2) mature reconstructions are likely at a lower risk of new invasions than younger reconstructions but are not immune, especially when invasive plants are present nearby and management does not occur, (3) sustained management is important to maintain low levels of invasive plant abundance; otherwise established populations rapidly expand, (4) forb abundance may be impacted by broadleaf-specific herbicide treatments, but the impact to the entire plant community is also at risk when invasive populations are not controlled, and (5) the invasive seed bank corresponds to aboveground abundance which is suppressed when management is sustained, likely reducing reinvasion risk. Taken together, our findings indicate that *Sericea lespedeza*, when established in a reconstructed prairie landscape, requires sustained management to maintain populations at low levels. This suggests that functional eradication is unlikely for *Sericea lespedeza* in prairie reconstructions and in the absence of sustained management, *Sericea lespedeza* populations quickly expand. However, management can be prioritized based on reconstruction age and *Sericea lespedeza* presence. In some cases, such as later-successional prairie communities where *Sericea lespedeza* is rare or absent, skipping a year of treatment may allow for resources to be allocated elsewhere without substantial risk of invasion or population growth.

We anticipated that prairie reconstructions established via herbicide and overseeding would have a greater abundance of *Sericea lespedeza* than cropped reconstructions due to a reduced weedy seed bank in the cropped reconstructions and greater richness and diversity with age (Newbold et al. 2020). However, we did not detect differences in *Sericea lespedeza* presence or abundance

in association with differing reconstruction practices. This might be attributed to increased resource competition in reconstructions established via herbicide and overseeding retaining greater species richness and abundance upon the initiation of reconstruction compared to reduced richness and abundance but greater weedy plant control following cropping practices (Newbold et al. 2020). Alternatively, the lack of differences between reconstruction practices may demonstrate the success of sustained *Sericea lespedeza* control treatments after reconstruction, effectively reducing populations regardless of differences in initial conditions due to differing establishment approaches.

An important goal of prairie reconstructions is to develop a native plant community that confers resistance to invasion. In our study, older, established reconstructions had smaller populations of *Sericea lespedeza*. We suggest two likely reasons: (1) these reconstructions were managed for *Sericea lespedeza* control for longer periods of time, and (2) the later-successional plant community in older reconstructions developed increased biotic resistance, defined as a reduction in invader success due to attributes of the resident plant community (Levine et al. 2004). While both likely contributed to the lower abundance of *Sericea lespedeza* observed in the older reconstructions in our study, it is difficult to fully disentangle them when interpreting our results. When these reconstructions were initiated, they were the sole focus of management effort, but as new reconstructions were established through time, resources were needed for managing the additional acreage. The increased manager effort and longer period of invasive plant management may have effectively removed *Sericea lespedeza* from some areas in the established reconstructions. However, where *Sericea lespedeza* was initially present in established reconstructions, populations grew regardless of whether it was managed or not. Population sizes in managed plots may have grown due to challenges detecting small, isolated pockets of *Sericea lespedeza* among a well-established, diverse, and tall prairie community. Established reconstructions, even with *Sericea lespedeza* initially present, were slower to see increases in *Sericea lespedeza*

abundance than the younger reconstructions. The established reconstructions at PFCA have been actively managed and maintained to promote late-successional prairie communities and reduce *Sericea lespedeza* abundance for many years prior to the start of this study. This suggests that through active prairie management, these established reconstructions may have greater biotic resistance to new invasions and may constrain invader abundance even though such resistance is unlikely to completely impede *Sericea lespedeza* invasion if left unchecked (Levine et al. 2004). The temporal trends of our data suggest that missing 1 year of treatment, based on a lack of differences in the first 2 years of management exclusion, may allow for resources to be diverted elsewhere without substantial increases in population growth, especially in established reconstructions or areas where *Sericea lespedeza* is not present. Based on our findings, the prioritization for treatment on an annual basis would proceed as follows: young reconstructions where *Sericea lespedeza* is present > established reconstructions where *Sericea lespedeza* is present > young reconstructions where *Sericea lespedeza* is rare > established reconstructions where *Sericea lespedeza* is rare. However, more research is needed to guide managers on treatment intervals or when “pauses” are acceptable while still maintaining functional eradication.

Our study was designed to represent operational conditions and challenges with *Sericea lespedeza* control across a managed landscape. With sustained control efforts, our results show that managers are effectively limiting *Sericea lespedeza* populations to less than 5% coverage across the landscape of reconstruction ages. At PFCA, managers treat reconstructions twice during the growing season. This may increase landscape-level effectiveness by capturing plants when they are both small (early in the growing season) and large (later in the growing season), in addition to treating populations that may have been missed during the earlier treatment. Past studies have explored how timing and formulation of herbicide applications influence control of *Sericea lespedeza* populations, with findings indicating successful control occurs early in the growing season and/or at the flowering stage (Yonce & Skroch 1989; Altom et al. 1992; Jordan et al. 2002; Koger et al. 2002; Farris & Murray 2009). Most of these studies were conducted in abandoned or degraded pastures dominated by non-native warm-season grasses or in experimental field plots that were seeded with *Sericea lespedeza*, which does not reflect challenges associated with managing reconstructed prairies at operational scales, namely greater heterogeneity in the plant community and reduced ability to discriminate *Sericea lespedeza* from other plant species.

Management of *Sericea lespedeza* via herbicide and haying may have unintended negative impacts on forb populations while increasing graminoids, but in the absence of management, burgeoning *Sericea lespedeza* populations reduced both forb and graminoid abundance. The large size of *Sericea lespedeza*, which grows to 0.8–1.5 m in height, can shade out native tall-grass prairie vegetation (Brandon et al. 2004; Farris & Murray 2009; Allred et al. 2010). The negative impact of unmanaged *Sericea lespedeza* populations on forb and graminoid populations at the plot scale has been documented in other studies (McMillan et al. 2023b), as have associated decreases in

invertebrate communities (Eddy & Moore 1998). Although efforts are made to reduce non-target impacts by directing herbicide applications to control only the intended plant species and by using selective broadleaf-specific chemicals, these herbicides may release grasses and more herbicide-resistant forbs (Crone et al. 2009). Our results suggest that additional research is needed to determine the impact of broadleaved herbicide treatments on non-target forb communities. Non-target impacts of herbicides may include reductions in leaf area, biomass, and alterations in phenology or reproduction in the short term with long-term impacts to population viability occurring after repeated treatment (Rice et al. 1997; Crone et al. 2009). These impacts may be particularly concerning for rare or conservative species. The selection of more specific chemical formulations or treatment applications could mitigate some non-target impacts. For example, hand-held wick applications of herbicide could be used when the need for high target plant selectivity is required (Tunnell et al. 2006). Non-target risk from herbicide control must be weighed against the risk of increased invasion without management. Our results show that stopping *Sericea lespedeza* management resulted in reductions in forbs and graminoids that intensified through time, suggesting that some non-target loss may be an acceptable trade-off for limiting *Sericea lespedeza* invasions and the cascading community effects resulting from such invasions.

Sericea lespedeza is a heavy seed producer, with estimates of 480–950 kg of seed produced per hectare in a pure stand, with about 770,000 seeds/kg (Cummings et al. 2017). It has been documented to have a persistent seed bank that is viable for several years (Barnewitz et al. 2009), although determining the exact time frame requires further investigation (Gucker 2010). *Sericea lespedeza* can reproduce by seed, but research suggests that seedlings are weak competitors (Farris & Murray 2009). It can also spread vegetatively from perennial root crown buds and possibly by root sprouting (McKee & Hyland 1941; Jordan et al. 2002). Our findings indicate that management of *Sericea lespedeza* aboveground corresponds to reduced levels of *Sericea lespedeza* seeds in the soil seed bank. Although this result suggests that management can affect the *Sericea* soil seed bank, due to the lack of pre-treatment data, we limited the ability to adequately quantify its impact. However, in a study investigating the effect of non-chemical approaches to minimizing *Sericea lespedeza* seed bank densities, mowing was found to significantly reduce the seed bank when compared to goat browsing (Barnewitz et al. 2009). In a *Sericea lespedeza* seed addition study, restored prairie plots that harbored higher species richness, cover, and functional guild diversity with lower bare-ground cover than abandoned hayfield plots had higher biotic resistance to substantial propagule pressure (400 seeds/1 m²) (Foster et al. 2015). Thus, continuing to manage aboveground vegetative structures of *Sericea lespedeza* will help to reduce the seed bank both through new seed additions and reductions in soil seed viability, which are likely less competitive as reconstructed prairies mature.

Guidance for *Sericea lespedeza* Management

This study suggests that in a landscape of mixed-age prairie reconstructions, managers can operationally control *Sericea*

lespedeza to 2–5% of ground cover by using combinations of repeated herbicide, haying, and fire. Although the landscape may have varying degrees of invasion, the efficacy of control efforts is evident when management is removed. *Sericea lespe-deza* populations increase, and the abundance of native herba-ceous plants decreases in the absence of management, an effect which is larger than non-target impacts to native plants caused by management. Despite the clear benefits of active management, challenges remain for field staff who feel as though they are constantly battling invasive plants and administrators who wonder if continued resources are needed when populations appear controlled. In a survey conducted by Rowe (2010), a majority of prairie managers indicated that their efforts to control invasive plants, which they believed were a moderate to severe threat to tallgrass prairies, were effective to highly effective. However, economic resources, including labor, were listed as significant impediments to successful invasive plant management. Our study suggests that (1) sustained management is effective in reducing impacts by *Sericea lespe-deza* across prairie reconstructions of varying ages, (2) investment in resources for *Sericea lespe-deza* control is important, and (3) operationally, managers have some flexibility to prioritize treatments or skip years based on reconstruction age and *Sericea lespe-deza* presence. Based on observations and lessons learned from the results of this study, we have the following suggestions for *Sericea lespe-deza* management:

- *Sericea lespe-deza* is slower to grow in the early growing season in comparison to native vegetation that may be overtopping it. This should be considered when deciding where to treat and when to monitor populations. Treating too early in the growing season and only once annually may miss stems that were covered by other vegetation or lead to non-target impacts. Additionally, consider surveying for the following year in the late-growing season when *Sericea lespe-deza* is easily detectable as it is generally taller than surrounding vegetation. Aerial detection of *Sericea lespe-deza* is also possible with hyperspectral imagery (Wang et al. 2008). Dormant-season ground surveys are also possible because the dead stems of *Sericea lespe-deza* are easy to identify.
- Large *Sericea lespe-deza* populations may require management beyond herbicide due to legacy effects from invasion (i.e. allelopathic compounds that can negatively impact the germination and growth of other plants) with a plan that incorporates a community-level approach (Munné-Bosch & Santos 2024).
- In mature prairies with small, isolated *Sericea lespe-deza* populations, detection might be challenging. Consider recording locations of known populations and maintaining an up-to-date database for retreatment and continued monitoring.
- Later-successional communities where *Sericea lespe-deza* is absent or well-controlled may allow for greater flexibility in the frequency of monitoring and treatment.
- Although *Sericea lespe-deza* populations may be more abundant in young (4–7 years old) reconstructions, the dominance of tall, native warm-season grasses at this stage may obscure populations, especially earlier in the growing season. Consider implementing transect treatment intervals within reconstructions to ensure detections between intervals will be observed.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Model effects for the percent coverage of *Sericea lespedeza* by management condition, restoration age class, and sample year.

Table S2. Means and standard error for the percent coverage of *Sericea lespedeza* by management condition, restoration age class, and sample year.

Figure S1. Change in *Sericea lespedeza* abundance by the initial coverage of forbs (panel A) and graminoids (panel B) and the change in forbs (panel C) and graminoids (panel D) over the 5-year study period by treatment.

Figure S2. Change in *Sericea lespedeza* abundance by the initial coverage of forbs (left panels) and the change in forb coverage over the 5-year study period by treatment and for each of the reconstruction age classes.

Figure S3. Change in *Sericea lespedeza* abundance by the initial coverage of graminoids (left panels) and the change in graminoid coverage over the 5-year study period by treatment and for each of the reconstruction age classes.