

Associating plant community composition and forage quality with soil fertility and seedbank
dynamics in managed Kansas rangelands

by

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Abstract

This thesis investigates population and community-level ecology in eastern Kansas rangelands, emphasizing the interconnected effects of fire, grazing, and herbicide treatments on aboveground plant community composition, forage quality, soil fertility, and the soil seedbank.

Chapter 1 provides a literature review exploring how fire and grazing shape plant community composition and seedbank dynamics. Chapter 2 examines relationships among aboveground plant community composition, forage quality, soil nutrients, and seedbank composition in a two-season field study comparing areas dominated by native perennial grasses (“grass-dominated”) with areas dominated by early-successional forbs, woody plants, or bare ground (“disturbed”). Disturbed areas exhibited higher levels of soil nutrients (nitrate, phosphorus, potassium), higher soil organic matter and carbon-to-nitrogen ratio, greater seedbank abundance and diversity, higher crude protein, and greater residue cover. Analyses of covariance were also performed to evaluate associations between soil and plant characteristics without differentiating grass-dominated from disturbed areas. These analyses were mostly non-significant. These findings illustrate the potential for qualitative vegetation surveys to provide some insight into complex ecological processes.

Chapter 3 used Uncrewed Aerial Vehicles (UAVs) to apply herbicide treatments and monitor herbicide efficacy. We evaluated impacts on mature plants, including Baldwin’s ironweed (*Vernonia baldwinii*), goldenrod (*Solidago* spp.), leadplant (*Amorpha canescens*), western ragweed (*Ambrosia psilostachya*), and white sagebrush (*Artemisia ludoviciana*) as well as potted seedlings, including alyssum (*Lobularia maritima*), Baldwin’s ironweed, common evening primrose (*Oenothera biennis*), common milkweed (*Asclepias syriaca*), and sericea lespedeza (*Lespedeza cuneata*). A lower rate of PastureGard®HL (0.21 kg ae ha⁻¹ triclopyr +

0.067 kg ae ha⁻¹ fluroxypyr) effectively suppressed some weeds at the seedling stage while minimizing non-target impacts. The recommended rate (0.63 kg ae ha⁻¹ triclopyr + 0.21 kg ae ha⁻¹ fluroxypyr) controlled both mature and seedling plants.

Chapter 4 is a pilot study aiming to develop a method for seedbank quantification in *sericea lespedeza*. The seeds of this species exhibit physical dormancy, which must be broken prior to greenhouse emergence assays. We tested several seed coat scarification methods including heating to 79 C, 107 C, or 204 C; 2 or 20 freeze-thaw cycles; and mechanical abrasion with sandpaper. This pilot study suggested that 20 freeze-thaw cycles would be the preferred method, although further replication is needed.

Collectively, these findings emphasize the importance of integrating aboveground with belowground data, and management practice with ecological process. This research supports more informed, integrated vegetation and weed management strategies for sustaining rangeland productivity and resilience.

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Dedication

I would like to dedicate this achievement to my family, my parents Chad and Karla, and my sister Brooke, whose constant support and encouragement have been the foundation of my academic journey. I am beyond blessed and grateful for the countless phone calls filled with love, motivation, and reassurance. Thank you for always being there for me.

Preface

Rangelands occupy an estimated 54% of global land area and play a vital role in providing ecosystem services worldwide (ILRI et al., 2021). These ecosystems are shaped by both natural and anthropogenic disturbances, including fire, grazing, drought, and herbicide application. Prescribed fire, livestock grazing, and herbicide treatments are widely used management tools that directly alter aboveground vegetation (Deng et al., 2014; Fuhlendorf et al., 2017; Limb et al., 2016; Metera et al., 2010). The effects of disturbance in the plant community extend belowground, influencing soil nutrients and the soil seedbank. The long-term sustainability of rangelands depends on effectively controlling problematic weeds and their seedbanks while maintaining productivity and ecologically beneficial native plant communities.

Rangeland condition is commonly assessed visually based on simple plant functional groups (e.g., grass, forbs, woody plants) and the amount of bare ground. While these aboveground indicators guide management decisions, they often overlook belowground processes that influence long-term plant community dynamics. Notably, the soil seedbank functions as a survival strategy for many rangeland plants adapted to recurrent disturbance (Briske, 1996; Ruprecht et al., 2017). Seed germination requires adequate soil nutrients, moisture, and light (Finch-Savage et al., 2006). Disturbances such as fire and grazing can reduce aboveground competition and increase resource availability, thereby influencing recruitment from the seedbank (Korfanta et al., 2015; Krueger-Mangold et al., 2006; Sheley et al., 1996). Over time, repeated and heavy disturbance can shift both aboveground vegetation and seedbank species richness and abundance, often favoring early-successional or weedy species (Mi et al., 2024; Shi et al., 2022; Towne, 2002; Vermeire and Gillen, 2000).

To actively manage aboveground vegetation, herbicide applications using Uncrewed Aerial Vehicles (UAVs) are becoming increasingly common in rangeland management. Although aerial herbicide application improves accessibility and operational efficiency, it also raises concerns regarding herbicide drift and potential non-target impacts on ecologically beneficial native forbs. Both positive and negative effects can occur when UAVs are used to target undesirable species such as sericea lespedeza [*Lespedeza cuneata* (Dum. Cours.) G. Don], a noxious invasive rangeland weed in the United States (Gucker, 2010; Wong et al., 2012).

Sericea lespedeza produces a persistent soil seedbank that can remain viable for 20 to 30 years due to its hard seed coat (Czarapata, 2005; Fitzgerald et al., 2005). For this reason, successful aboveground control does not necessarily prevent future reinvasion. Accurate seedbank quantification is therefore critical. Soil seedbanks are typically assessed through seedling emergence assays or by extracting seeds from soil samples (Mahé, 2021). Emergence methods may underestimate species with dormant seeds that fail to germinate under greenhouse conditions. This limitation is particularly relevant for sericea lespedeza, which exhibits strong physical dormancy. Laboratory scarification treatments, such as heat exposure, freeze-thaw cycles, or mechanical abrasion, can simulate natural dormancy-breaking processes and improve germination for better seedbank quantification (Blocksome, 2006; Graham, 1945; Gucker, 2010; Segelquist, 1971).

The overarching objective of this thesis was to explore how aboveground management practices and plant community dynamics interact with belowground processes in tallgrass prairie. I place particular emphasis on soil seedbanks, soil nutrients, and vegetation responses to disturbance and management practices. The thesis consists of four chapters with the following objectives:

- Chapter 1: To synthesize existing knowledge on how grazing and fire modify soil seedbank dynamics in rangeland ecosystems.
- Chapter 2: To evaluate how differences in aboveground plant communities correspond with differences in forage quality, soil seedbanks, and soil fertility.
- Chapter 3: To evaluate the efficacy and non-target effects of UAV-applied triclopyr + fluroxypyr at two rates, applied to weeds and desirable plants at two growth stages.
- Chapter 4 Objective: To compare laboratory methods for stimulating germination of sericea lespedeza seeds within an artificial soil seedbank.

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Chapter 1

Impacts of livestock grazing and prescribed fire on rangeland seedbanks: A review

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Keywords: disturbance, grazing, herbivory, prescribed fire, rangeland ecology, soil seedbank

Introduction

Rangelands occupy an estimated 54% of global land area, playing an essential role in the provision of ecosystem services worldwide (ILRI et al., 2021). Many rangeland ecosystems are maintained by a combination of natural and anthropogenic disturbances, which jointly serve to limit the progress of secondary succession (S. R. Archer et al., 2017; S. Archer & Stokes, 2000; Belsky, 1992; MacDougall & Turkington, 2007). Natural disturbances include wildfires, extreme weather events, and grazing from wild animals. Key anthropogenic disturbances are related to livestock grazing patterns and prescribed fire.

Anthropogenic disturbances have immediate, visible effects on aboveground plant communities (Deng et al., 2014; Fuhlendorf et al., 2017; Limb et al., 2016; Metera et al., 2010). These effects include changes in measures of abundance, including plant density, biomass, and height. They also include changes in plant species composition and diversity. Notably, livestock grazing favors plant species and ecotypes that can either avoid or tolerate aboveground damage (D. D. Briske, 1996; Matches, 1992; Noy-Meir et al., 1989). Grazing avoidance traits include phenological, morphological, and physiological characteristics. Grazing tolerance reflects factors such as apical meristem location and the form, amount, and timing of belowground carbohydrate storage. As grazing intensity increases, plants that are unable to avoid or tolerate grazing are removed, reducing competitive pressure against more grazing-resistant species and potentially increasing their representation in the plant community (Bat-Oyun et al., 2016; García et al., 2020; Koerner et al., 2018; Segre et al., 2016), although this pattern does not always occur (Y. Li et al., 2025). Additional early-successional and grazing-resistant species may also appear in the community.

Similarly, prescribed fire not only removes aboveground biomass but also serves as an ecological filter governing the process of plant community assembly. Like grazing resistance, fire resistance can involve both avoidance and tolerance (Enright et al., 2014; Pausas, 2019; Vesk, 2006). An example of fire avoidance would be an annual plant that completes its life cycle and produces seeds prior to a prescribed fire. Early-successional plants, including annuals, may thrive in fire-prone rangelands because these fast-growing, disturbance-adapted species capitalize on post-fire resource availability to recolonize the area (Brooks, 2002; Keeley, 2006; Pyke et al., 2010). Many perennial plants occupying fire-prone landscapes instead exhibit fire tolerance, meaning the capacity for recovery following fire (Moore et al., 2019; Pyke et al., 2010). Recovery depends on factors including the timing and intensity of fire as well as interactions with other stressors, including grazing.

The aboveground impacts of grazing and prescribed fire regimes are well documented, albeit very context-dependent. However, the impacts of these practices on the soil seedbank are often overlooked. Livestock grazing and prescribed fire may modify the abundance, diversity, and species composition of viable seeds in the seedbank, but these effects are not necessarily parallel to trends occurring aboveground (Chick et al., 2015; Kushbokov et al., 2025; Mi et al., 2024; Shi, Shi, Huang, et al., 2022; Shi, Shi, Jiang, et al., 2022). Given the ecological importance of the soil seedbank in serving as a buffer against environmental variability (DeMalach et al., 2021; Kiss et al., 2018; Plue et al., 2021; Vandvik et al., 2016), it is important to understand ways in which our rangeland management decisions alter seedbank dynamics. The goal of this article is to provide an accessible review of key pathways by which management decisions alter the seedbanks of both desirable and undesirable plants.

Livestock Grazing

The effects of grazing on plant communities depend on numerous factors, including livestock species, behavior, grazing intensity, and duration and timing of grazing (Bailey et al., 1996; Bakker, 1998; Hodgson et al., 1994). These factors modify soil seedbanks as well as aboveground plant communities (Figure. 1.1) (Hendrickson & Olson, 2006). Global meta-analyses by Shi et al. (2022) and Mi et al.(2024) have examined how grazing impacts the soil seedbank. Shi et al. (2022) tested the impacts of grazing on seedbank abundance, richness, and compositional similarity between the aboveground vegetation and the seedbank. They found that grazing reduced seedbank abundance. Seedbank richness increased with low-intensity grazing but decreased with high-intensity grazing (Shi, Shi, Huang, et al., 2022). Mi et al.(2024) also reported that grazing reduced seedbank abundance, especially for perennial plants. Grazing also reduced taxonomic diversity by some measures, with these effects depending on grazing intensity and duration (Mi et al., 2024). Both studies reported that grazing had more negative impacts on seedbanks in arid areas (Mi et al., 2024; Shi, Shi, Huang, et al., 2022). As a disturbance, grazing influences seed bank dynamics by shaping fundamental processes such as seed rain, dispersal, persistence, and germination.

Seed Rain

Although seeds can be removed from soil seedbanks in several ways, including decay, predation, fatal germination, and successful establishment, they can only enter seedbanks in two ways: seed production by nearby plants or seed dispersal into the area (Leck et al., 2012). Seed production by nearby plants is often the dominant pathway. For that reason, grazing patterns that reduce seed production can significantly reduce seedbank abundance (Figure. 1.1).

Avoiding grazing during the reproductive periods of key plant species could help preserve the seedbanks of those species (Noy-Meir & Briske, 1996). A three-year grazing study in a Mediterranean grassland in Israel found that heavy late-season grazing reduced seed production, especially of annual species, compared with grazing earlier in the growing season (Sternberg et al., 2003). Some rest rotational grazing systems are designed to enable substantial seed production by forage species every few years (USDA NRCS, 2022). In other areas, livestock grazing is continuous but limited to a few months of the year, which can potentially be carried out prior to the reproductive periods of dominant forages. This approach is aligned with livestock productivity goals because forage plants are generally most nutritious and digestible in vegetative rather than reproductive stages. When the dominant forages are warm-season grasses, such grazing regimes will tend to end in midsummer, e.g., intensive early stocking in the Great Plains of North America (Smith & Owensby, 1978). These grazing regimes may disadvantage cool-season species that are trying to set seed during the grazing period.

In addition to the timing of grazing, managers have opportunities to manipulate plant communities by modifying the grazing intensity (Herrero-Jáuregui & Oesterheld, 2018; J. L. Holechek & Galt, 2000). Grazing intensity across the entire managed range area is primarily a function of plant productivity and stocking rate, but the effects of grazing in any particular location also reflect the evenness of grazing distribution across space and consistency over time (Bailey, 2004; Bailey et al., 1996; J. Holechek et al., 2011; Jablonski et al., 2024). Relatively light grazing may not change total biomass production (compensation), or in some cases may even increase biomass production (overcompensation) (A. K. Knapp et al., 2012; Noy-Meir, 1993; Ramula et al., 2019). However, even in these cases, it is possible that plant reproduction will be affected by grazing (Hickman & Hartnett, 2002; Wentao et al., 2023). With heavier

grazing, it is more likely that a plant's ability to produce seeds will be reduced. Seeds may also exhibit maternal effects reflecting the grazing history of the parent plant (Roach & Wulff, 1987). Although seed rain is the direct deposit of seeds into the soil seedbank, seeds entering the seedbank can be first dispersed through livestock vectors.

Seed Dispersal

In addition to seed rain from local plants, the other mechanism by which seeds enter the soil seedbank is dispersal (Leck et al., 2012). Long-distance dispersal may be carried out by abiotic factors such as wind and water, by humans, or by animals (D. R. Murray, 2012). Among animals, livestock often play important roles in distributing seeds across the landscape (Figure. 1.1) (Auffret & Cousins, 2013; Chuong et al., 2016; Cosyns et al., 2005; Hogan & Phillips, 2011).

Seeds may be ingested and deposited in dung (endozoochory) or attached to fur or skin (exozoochory or epizoochory). A study on endozoochory by Scottish Highland cattle and Shetland and Konik horses in coastal dunes of Belgium found that 59,049 seedlings of 117 species emerged in the greenhouse from 51 collected dung samples (Cosyns et al., 2005). In Oregon, United States, fecal samples from cattle had more germinable seeds than samples from elk and deer (Bartuszevige & Endress, 2008). Intake and diet selectivity likely contributed to these trends. Relatedly, cattle have a long retention time of forage and seeds, which could enhance the scarification and germination of hard-coated seeds at the cost of lower seed survival (Nikolić et al., 2025). There were more exotic grasses found in cattle dung compared with the native ungulates; elk had a greater proportion of forbs and shrubs than cattle (Bartuszevige & Endress, 2008). These trends reflect dietary differences between cattle, elk, and deer, potentially

combined with differences in the digestibility of native seeds in the cattle rumen, higher fecundity of exotic grass seeds, or that exotic seeds are smaller and less likely to be damaged in cattle rumen (Bartuszevige & Endress, 2008).

In contrast with endozoochory, epizoochory often relies on seed traits such as hooks or awns allowing seeds to latch onto passing animals (Couvreur et al., 2008; D. R. Murray, 2012). Small seeds without these morphological adaptations may also become tangled in fur (Rosas et al., 2008). In annual grasslands of California, United States, Chuong et al. compared the seed content of cattle dung versus seeds found on cattle fur upon return from a pasture containing annual invasive grasses including medusahead (*Taeniatherum caput-medusae*) (Chuong et al., 2016). Invasive species were more likely to be dispersed by epizoochory and forbs in general were more likely to be dispersed by endozoochory (Chuong et al., 2016). Rosas et al. (2008) found that bison, both a native herbivore and a livestock species, also disperse several non-native plant species in their fur, such as bromes (*Bromus* spp.) and hedge parsley (*Torilis arvensis*).

Seed Persistence

Unlike aboveground plant communities, which change relatively quickly, seedbanks change more slowly and reflect long-term “memory” of grazing regimes. The strength of this legacy depends on the longevity and persistence of the seeds in the seedbank (Kiss et al., 2018; Ma et al., 2021). Soil seedbank persistence is associated with environmental conditions (abiotic and biotic) and multiple seed traits, including not only physiological characteristics but also morphological ones such as seed size and seed shape (Hulme, 1998; Ooi, 2012; Thompson et al., 1993; Zinsmeister et al., 2020). An analysis by Wang et al. (2024) compiled a worldwide dataset of seed persistence for 1474 species from 650 genera and 112 families across 23 geographic

locations. Using a three-dimensional variance equation yielding a measure of seed shape (Bekker et al., 1998), seed shapes ranged from very spherical [(0.0001 in African mustard (*Brassica tournefortii*)] to elongated or disk shaped [(0.33 in European feather grass (*Stipa pennata*)] (Wang et al., 2024). Among herbaceous species, smaller, more spherical seeds were found to be more persistent in the soil seedbank (Wang et al., 2024). These seeds are more likely to be moved deeper into the soil profile by rainfall, animal activity, freeze-thaw cycles, soil erosion, and human interventions. In contrast, larger, less-spherical seeds are more likely to remain in the upper layers of the soil due to frictional forces. In these upper layers, they are both more vulnerable to death and more likely to successfully germinate (Wang et al., 2024).

In the context of rangeland management, the presence and persistence of desirable species in the seedbank help determine the potential for natural regeneration of a degraded area (Bossuyt & Honnay, 2008; Rayburn et al., 2016; Shiferaw et al., 2018; Skoglund, 1992). For instance, if an invasive weed arrives but is rapidly controlled with herbicides that also remove resident species, the resident species may be able to re-establish from the existing seedbank. However, control of a long-established weed population may need to be followed by reseeding. Herbaceous weed species also form seedbanks, and in fact may exhibit greater seedbank persistence than later-successional, more desirable rangeland species (DiTomaso, 2000; Grundy & Jones, 2002; Renne & Tracy, 2007). Weed seeds are potentially long-lived and exhibit substantial seed dormancy, allowing them to remain viable for years until environmental conditions are suitable for establishment (Baker, 1974). Persistent weed seedbanks are present even in grasslands with mostly desirable vegetation. The presence of noxious weeds in the seedbank necessitates increased scouting effort over the long term.

Seed Germination and Establishment

Persistent soil seedbanks may be reduced through death or germination of the seeds (Leck et al., 2012). Grazing livestock modify these processes by changing the soil environment, altering factors such as temperature, light, soil moisture, and nutrient availability. Such factors are important determinants of dormancy states and germination rates (Finch-Savage & Leubner-Metzger, 2006). By removing aboveground vegetation, grazing livestock may expose seeds to warmer and more variable temperatures with increased light availability, increasing the likelihood of seed germination and availability of safe sites for establishment (Bullock et al., 1994; Kladivová & Münzbergová, 2016; Oosterheld & Sala, 1990). Additional mechanisms through which livestock change soil environments are trampling and nutrient addition (Figure. 1.1).

Trampling and hoof action create new microenvironments that expose some seeds to conditions more favorable for germination. Notably, these processes can help bury surface-lying seeds and increase seed-to-soil contact. They can also help release seeds deposited in herbivore dung (Faust et al., 2011). A study on species from European open inland sand ecosystems used a synthetic hoof to assess the germination response of surface-lying seeds to simulated sheep trampling (Eichberg & Donath, 2018). The authors found a positive effect of trampling on seedling emergence (Eichberg & Donath, 2018). Trampling also reduced time to germination, increased germination synchrony, and increased aboveground biomass. These trends were stronger in ruderal species, which are adapted to disturbance (Eichberg & Donath, 2018). Another study compared the potential of cattle trampling or mechanical preparation (land imprinting or ripping) to bury native grass seeds broadcast on the soil surface in Arizona, United

States (Winkel & Roundy, 1991). Heavy trampling and the mechanical preparation methods all led to greater seedling emergence compared with no disturbance or light trampling.

Grazing livestock deposit nutrients as dung and urine, fertilizing growing plants and modifying patterns of seed germination (Dahlin et al., 2005; Dai, 2000; Pavlů et al., 2019; Scheile et al., 2018). A study in Japan observed a doubling of aboveground zoysia grass (*Zoysia japonica*) biomass within 10 cm of dung patties (Yoshitake et al., 2014). A laboratory experiment on Khirni (*Manilkara hexandra*) found that seed germination rate increased from 28% to 66% when the seeds were mixed in cattle urine for 12 hours and a dung slurry for 12 hours (Shinde & Malshe, 2015). In addition, time-to-germination decreased from 20 to 15 days and seedlings from the treated group had greater plant height, number of leaves, primary root length, and number of tertiary roots (Shinde & Malshe, 2015). In a lightly grazed limestone grassland in Sweden, the longer the soil was covered by cattle dung, the smaller the proportion of transient seeds relative to long-term persistent seeds in the soil seedbank (Dai, 2000). The same study also reported differences in how species responded to dung patches at different degradation stages. Certain species, like meadow oat-grass (*Helictochloa pratensis*) and five-stamened chickweed (*Cerastium semidecandrum*), responded positively to dung at the edge of the dung patch. Other species, like brown bentgrass (*Agrostis vinealis*) and hoary rockrose (*Helianthemum oelandicum*), did not change in cover with distance to the dung patch. A third group of species, including kidney vetch (*Anthyllis vulneraria*) and sedges (*Carex* spp.), were negatively impacted by the dung patch (Dai, 2000). Overall, these studies show that the effects of fertilization by dung and urine are species-specific but that dung and urine frequently enhance recruitment and growth in nutrient-limited rangelands.

Prescribed Fire

Many rangelands around the world have historically been maintained by fire, which serves to support productivity and biodiversity of fire-adapted vegetation (Limb et al., 2016; Twidwell et al., 2021). Preventing wildfire in these landscapes can be important to protecting human lives and livelihoods but also contributes to problems such as invasive species and woody encroachment (Archer et al., 2017). As an alternative, managers can implement prescribed fires to maintain healthy landscapes and support ecosystem services, including livestock productivity (Francos & Úbeda, 2021; Fuhlendorf et al., 2011; Limb et al., 2016). In the long term, prescribed fire results in modifications to the soil seedbank. These modifications may reflect effects of prescribed fire on seed production, seed mortality, or seed germination (Figure. 1.2).

Seed Production

Prescribed fire is often applied during times when perennial forage plants are dormant. This timing enables the plants to recover during the entire growing season, often producing additional ramets after the fire. The initial removal of aboveground biomass reduces vegetative cover and increases light availability at the soil surface as well as the availability of other resources, enhancing recruitment and subsequent growth of some species (Berleman et al., 2016; Franzese et al., 2009; Zimmermann et al., 2008). This effect could result in a greater number of species contributing to the seedbank, perhaps especially at moderate fire frequencies (intermediate disturbance hypothesis) (Gordijn & O'Connor, 2021; He et al., 2019; Valkó et al., 2016).

Fire timing and frequency alter the relative abundance of different plant functional types (Fig. 1.2). Plants with non-dominant phenologies may be negatively affected by a fire timed to

support dominant forages (e.g., cool-season species in a mostly warm-season grassland burned in spring) (Howe, 1994; E. Knapp et al., 2009). Repeated annual spring prescribed fire also tends to increase the abundance of grasses relative to forbs (Benson et al., 2004; Dalgleish & Hartnett, 2009). Plumanns-Pouton et al. (2024) used plant functional types to develop a framework predicting the effects of fire frequency on plant relative abundance. They found that broad classifications of obligate seeder, facultative resprouter, and obligate resprouter were not sufficient to explain variation in plant responses to fire. For instance, obligate seeders benefitted from short fire return intervals if they were quickly maturing and had short-lived seedbanks but necessarily in other cases (Plumanns-Pouton et al., 2024). Obligate resprouters were most likely to succeed at low fire frequencies, whereas facultative resprouters showed substantial variation that was associated with the rate of maturation and whether the plant resprouted to a juvenile or a mature state (Plumanns-Pouton et al., 2024).

In addition to changing seed production by desirable forages, prescribed fire can also suppress undesirable plants. Notably, prescribed burning can reduce the abundance of various early-successional weeds in climax rangeland communities (DiTomaso et al., 2006). Many of these weeds have high fecundity (Baker, 1974), so suppressing seed production may be important to preventing the development of large and persistent weed seedbanks. Frequent fires have been shown to reduce the seedbank size of various herbaceous annuals with long-lived seedbanks (Plumanns Pouton et al., 2024), a common functional category for rangeland weeds. However, there are also situation in which fire instead exacerbates problems with early-successional weeds, e.g., annual *Bromus* spp. (Bradley et al., 2018; Pilliod et al., 2017).

In addition to herbaceous weeds, many trees and shrubs contributing to woody encroachment are also suppressed by frequent fire (J. Li et al., 2022; Lohmann et al., 2014;

Miller et al., 2017; Symstad & Leis, 2017). In the eastern tallgrass prairie of North America, an increase in fire frequency will support biodiversity and stabilize late-successional prairie plant communities, partially due to the removal of trees and shrubs (Bowles & Jones, 2013). The extent to which these trends will be reflected in woody plant seedbanks depends on the woody species in question. Woody species generally form smaller, more transient seedbanks than herbaceous plants; however, non-sprouting, fire-killed woody species produce more seeds than sprouting woody species (El-ahmir et al., 2015).

Seed Mortality

Prescribed fire generally causes some seed mortality without eliminating the entire seedbank (Figure. 1.2) (E. Knapp et al., 2009).

Fire intensity depends largely on the amount of fuel available and the characteristics of available fuel, such as moisture and density (Hiers et al., 2020; E. Knapp et al., 2009). In a study in the Patagonia steppe, prescribed fire intensity was manipulated by adjusting the biomass on the soil surface (Gonzalez et al., 2022). The authors found that exposure to low and high fire intensities, occurring at 390 g m⁻² and 610 g m⁻² of biomass, respectively, decreased germination of most species. These effects were stronger with the high fire intensity. The authors concluded that long exposure to temperatures above 60 C generally had lethal effects on seeds (Gonzalez et al., 2022).

Seed location in the soil profile reflects seed morphology and the extent to which the soil is being disturbed, whereas seed characteristics governing fire resistance include both morphological and developmental traits. Seedbank research in northwest Patagonia demonstrated that seeds of all tested annual species survived fire but only two perennial species survived

(Gonzalez & Ghermandi, 2008). Annual species had smaller seeds, which aided them in getting deeper into the soil for protection (Gonzalez & Ghermandi, 2008). In contrast, perennial species seedbanks were adversely affected by fire but showed signs of recovery in the third year (Gonzalez & Ghermandi, 2008). At any given location in the soil profile, seeds with harder seed coats, lower moisture content, and rounded shapes are likely to have greater fire survival (Rolston, 1978; Ruprecht et al., 2015; Tangney et al., 2019). Other relevant factors include the position of the embryo in the seed and propagule structures including the lemma, palea, and pubescence (Gonzalez et al., 2022).

Seed Germination

Scarification, heat, and smoke chemicals can enhance germination in fire-adapted plants (Figure. 1.2). Some seeds benefit from fire to scarify their seed coats, which releases physical dormancy in hard-seeded species (Baskin & Baskin, 2014; Rolston, 1978). For example, in the Patagonian grassland species pichi (*Fabiana imbricata*), germination was enhanced by scarification in combination with smoke and heat (Dudinszky & Ghermandi, 2013). In the tallgrass prairie of North America, the germination of the invasive species sericea lespedeza (*Lespedeza cuneata*) is enhanced by fire due to scarification of the hard seed coat (Wong et al., 2012). This trend helps explain why late-spring prescribed burns, a common management practice in the region, may exacerbate *L. cuneata* infestations unless paired with well-timed weed control measures. In contrast, summer or fall prescribed burns help suppress this invasive weed and limit seed production (Alexander et al., 2021).

Smoke is another important driver of enhanced germination after fire. An experiment in the Cerrado of central Brazil demonstrated that when some species overcome physiological

dormancy, they become sensitive to smoke cues that enhance germination and seedling growth (Ramos et al., 2019). Riparian three-awn (*Aristida riparia*) and curved three-awn (*Aristida recurvata*) had especially positive responses to smoke (Ramos et al., 2019). In another experiment, seeds were collected from 20 native grass species in New South Wales, Australia, to observe the impact of smoke on germination (Read & Bellairs, 1999). Smoke stimulated germination in nearly half the species; in other species, it modified time to germination without changing germination percentage or had no effect (Read & Bellairs, 1999).

Future Directions

Livestock grazing and prescribed fire regimes have been extensively studied in many world regions. However, most data collection has focused on aboveground plant communities. Effects of grazing and fire on plant seedbanks can be harder to predict, especially as these effects can occur through multiple pathways. Livestock grazing impacts seed rain from existing plants, seed dispersal from other ecosystems, seed persistence in the seedbank, and seed germination. Prescribed fire impacts seed production, mortality, and germination. The combination of these different factors can lead to unexpected impacts on soil seedbanks that are often not directly parallel to changes occurring aboveground. Given the importance of soil seedbanks in resisting compositional change and enabling recovery after disturbance (DeMalach et al., 2021; Plue et al., 2021), there would be great value in developing more accurate methods to estimate changes occurring in seedbanks. There is substantial potential for more mechanistic as well as empirical seedbank modeling (Eager et al., 2013, 2014, 2017; Merow et al., 2014; Peco et al., 1998; van Langevelde et al., 2016). We also highlight the potential of approaches based on plant functional

types (Plumanns-Pouton et al., 2024), which are more generalizable than species-specific approaches.

The development of seedbank models would be facilitated by a high-throughput, high-accuracy way to measure plant seedbank characteristics. Most seedbank assessments are carried out with greenhouse emergence assays, which are time-consuming and underestimate the prevalence of more dormant seeds, or physical extraction (elutriation, flotation, sifting) procedures, which underestimate the prevalence of small seeds and do not account for seed viability (Espeland et al., 2010; Mahé et al., 2021; Price et al., 2010). Emerging methods such as DNA profiling (Haring & Flessner, 2018; Viruel et al., 2025) are not yet cost-effective at scale. These obstacles limit data collection even in research contexts and render seedbank assessment impractical for most practitioners. The development of a reliable, quick, and economical method of seedbank assessment will be essential to improving our understanding of management effects on rangeland seedbanks.

Even as we develop a better understanding of grazing and fire effects on rangeland seedbanks, we are also increasing our capacity to apply that knowledge. Emerging technologies are enabling more precise approaches to rangeland management. For example, remote sensing strategies for range monitoring are increasingly widespread (Reeves et al., 2024; Retallack et al., 2023; Svoray et al., 2013). The resulting data are used to guide livestock grazing and prescribed fire decisions. These management practices may also be implemented in more precise ways, e.g., through the use of virtual fencing (Goliński et al., 2023; B. D. Murray et al., 2025; Schillings et al., 2024). Thus, if we can improve our ability to estimate seedbank dynamics (with models drawing on aboveground data, or with direct measurements), we can immediately use this

knowledge to enhance the economic and environmental sustainability of our range management practices.

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Figures

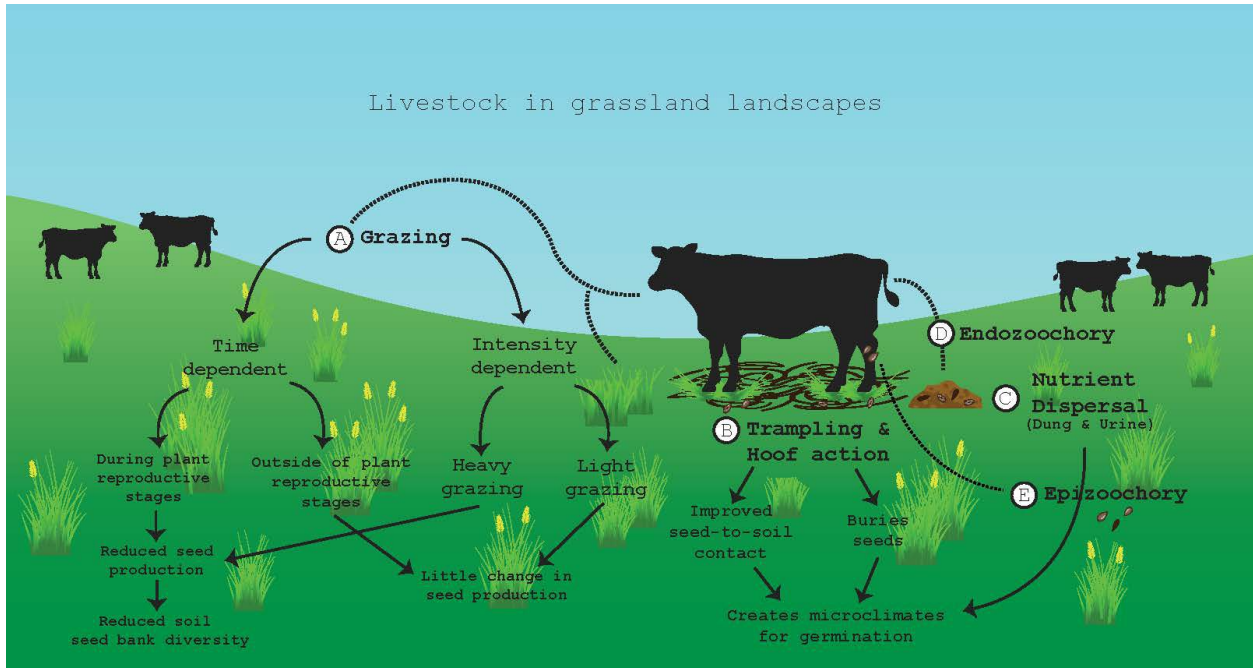


Figure 1.1. Effects of livestock grazing on rangeland soil seedbanks. Livestock grazing impacts seed rain from nearby plants, seed dispersal from neighboring ecosystems, seed persistence in the seedbank, and seed germination.

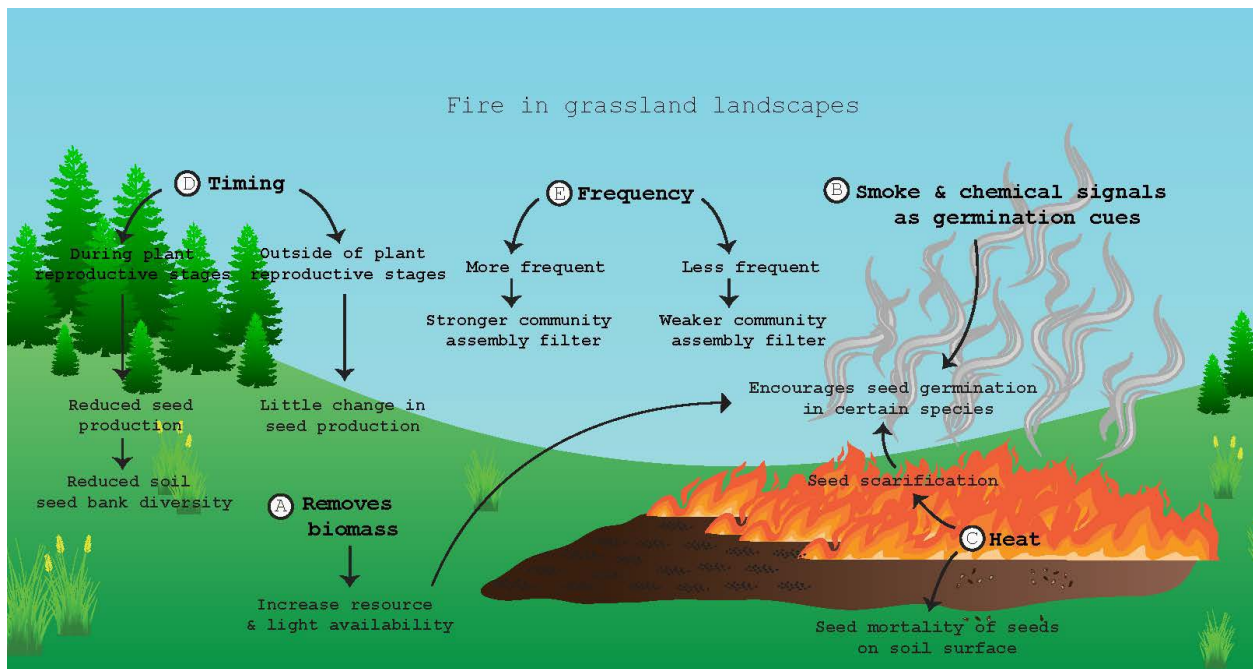


Figure 1.2. Effects of prescribed fire on rangeland soil seedbanks. Prescribed fire impacts seed production, mortality, and germination.

Chapter 2

Associations between aboveground vegetation, soil seedbanks, and soil properties in Kansas tallgrass prairie

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Abstract

Rangeland ecosystems are shaped by complex feedbacks between soil conditions, soil seedbanks, and aboveground vegetation. Many of these processes are difficult to observe directly, so land management decisions are often based on visual surveys of the aboveground vegetation. This study integrates aboveground with belowground measurements in native tallgrass prairie near Manhattan, Kansas, USA. We used visual surveys at the end of the grazing season to differentiate areas dominated by desirable native grasses (“grass-dominated”) from areas dominated by early-successional forbs, woody species, or bare ground (“disturbed”). The soil in disturbed areas had higher nitrate, phosphorus, and potassium concentrations, higher carbon-to-nitrogen ratio, and higher organic matter than the soil in grass-dominated areas. The seedbank in disturbed areas had higher abundance, species richness, and Shannon-Wiener diversity than the seedbank in grass-dominated areas ($P < 0.05$). Aboveground, disturbed areas had more litter on the soil surface and more crude protein in the vegetation. Analyses of covariance evaluating associations between soil and plant characteristics without differentiating grass-dominated areas from disturbed areas were mostly not significant. Overall, our results demonstrate strong connections between soils, seedbanks, and aboveground plant communities. For this reason, visual surveys of aboveground vegetation may be used to make predictions about other dimensions of range ecosystems. A multidimensional understanding of rangeland health will help optimize decision-making for sustained productivity.

Keywords: Community ecology, grassland, rangeland, soil fertility

Introduction

On grazing-based livestock operations, visual assessments of the aboveground vegetation are a crucial monitoring element for management decisions. These assessments are frequently informal (e.g., qualitative) in nature and conducted continuously throughout the year (Smith et al., 2025; Woods & Ruyle, 2015). Relative to more formal evaluation methods, informal visual assessments are perceived to be more time-efficient and relevant at the highly localized scales that are important to ranchers (Smith et al., 2025). For this reason, informal visual assessments play an important role in guiding localized management decisions (Smith et al., 2023, 2025) and informing the strongly place-specific mental models used by land managers (Puntenney et al., 2025). Even when informal monitoring is supplemented with more formal approaches, visual assessment remains an important part of the monitoring program (Stephenson et al., 2017).

Visual assessment of the aboveground vegetation is an effective way to gather information about some aspects of rangeland health. For example, managers may note the presence of bare ground, herbaceous weed species, or undesirable woody species. Bare ground, including bare ground resulting from overgrazing, has long been noted as a driver of erosion (Steiger, 1930; Weaver & Fitzpatrick, 1934). Herbaceous weed communities in rangeland environments include a wide range of species and functional types. Most rangelands in the U.S. Great Plains include some early-successional native weeds such as ragweed species (*Ambrosia* spp.). These plants usually exhibit ruderal life histories and increase in response to disturbance, so function as indicators of disturbance intensity (Towne, 2002; Vermeire & Gillen, 2000). However, controlling early-successional forbs does not necessarily result in enhanced livestock productivity (Fuhlendorf et al., 2009; Harmony et al., 2024). On the same Great Plains landscapes, more aggressive invasive plants may outcompete desirable native forages even in the

absence of external disturbance. Examples listed as Category C noxious weeds on Kansas rangelands include sericea lespedeza [*Lespedeza cuneata* (Dum.Cours.) G.Don] and musk thistle (*Carduus nutans* L.) (Kansas Department of Agriculture, 2022). Woody encroachment is among the greatest threats to Great Plains rangeland, partially due to the difficulty of reversing this process (S. R. Archer et al., 2017; J. Li et al., 2022; Miller et al., 2017; Symstad & Leis, 2017).

Although identifying bare ground, herbaceous weed species, or undesirable woody species can help guide management, these observations alone provide an incomplete picture of rangeland ecology and grazing potential. For example, livestock managers are interested in both the quantity and the quality of forage available in different areas across the rangeland. Forage quality is a multidimensional concept integrating the ideas of palatability, intake, digestibility, animal physiological status, and nutrient content (Ball et al., 2001). In general, replacement of native rangeland plants with invasive weeds is problematic partially because forage quality may be compromised (DiTomaso, 2000). However, the impacts of change to plant community composition on forage quality are species- and context-specific. Many ruderal species have fairly high nutrient content (Marten & Andersen, 1975; Weir et al., 2009), in line with the well-recognized ability of weeds to capitalize on available soil fertility (Zimdahl, 2018). In fact, some weedy rangeland species accumulate nitrates so effectively that they become toxic for this reason. Woody plants are generally not included in the diets of grazing cattle and sheep, so resource uptake by woody plants leads to reduced forage availability these grazers (Morford et al., 2022; Symstad & Leis, 2017).

Soil fertility is closely associated with plant community composition. Structured rangeland health assessments integrate soil with plant indicators, recognizing the many links between these elements of range ecosystems (Printz et al., 2014). In North America, many

rangelands are nitrogen-limited, especially at higher levels of water availability (Holechek et al., 2011; Symstad & Jonas, 2011). High levels of soil nitrogen availability can increase aboveground net primary productivity, thereby reducing light availability and plant diversity (Baer et al., 2003; Clark et al., 2007; Symstad & Jonas, 2011). In addition, variation in soil fertility alters the relative competitiveness of different plant functional types. Although many later-successional plants, including native warm-season forage grasses, are strongly competitive for nutrients, many ruderal species are able to rapidly capitalize on available resources (Korfanta et al., 2015; Krueger-Mangold et al., 2006; Sheley et al., 1996). Conversely, plant community characteristics influence soil characteristics and processes (Camill et al., 2004). For example, early-successional species may accelerate nutrient cycling (Krueger-Mangold et al., 2006; Yahdjian et al., 2017) while legumes add nitrogen to the soil (De Deyn et al., 2009; D. A. Johnson et al., 1981). Positive feedback loops between plant communities and soil fertility can magnify the impacts of change to rangeland ecosystems (S. Archer & Bowman, 2002; Jing et al., 2014).

Positive feedback loops also link changes to aboveground plant communities with changes to the soil seedbank. In rangeland environments, aboveground plant communities and soil seedbanks often show differences in their species composition (Coffin & Lauenroth, 1989; R. G. Johnson & Anderson, 1986; Zylka, 2016). Many late-successional rangeland plants are less reliant on seedbanks than more disturbance-adapted species, which frequently produce many seeds and exhibit high seed persistence (DiTomaso, 2000; Grundy & Jones, 2002; Renne & Tracy, 2007). A potential negative consequence is that invading early-successional weeds can produce large, persistent seedbanks, resulting in weed recruitment for years to come (DiTomaso, 2000; Grundy & Jones, 2002; Renne & Tracy, 2007). On the other hand, rangeland seedbanks

also have the potential to enhance resilience and facilitate recovery after disturbance by preserving a “memory” of past diversity (Fabšičová et al., 2024; Guo et al., 2023; Kiss et al., 2018; Thompson & Grime, 1979).

The objective of this study is to integrate visual surveys of aboveground vegetation with data on forage quality, soil fertility, and soil seedbanks. Understanding how these data types connect could help optimize long-term rangeland management for livestock production. For example, we may notice areas where visual surveys fail to recognize belowground seed reserves that drive weed recruitment or where soil nutrient heterogeneity generates substantial within-pasture variation in forage value.

We evaluated the relationships between aboveground and belowground parameters using two complementary approaches. First, we used an aboveground-driven approach in which visual surveys (mimicking producer monitoring) were used to identify paired “grass-dominated” and “disturbed” plots. The label “grass-dominated” was applied to areas with a high abundance of native warm-season grasses. The label “disturbed” was applied to areas with high levels of bare ground, early-successional forbs, and/or woody plants. According to this definition, the disturbed plots were generally in worse condition than the grass-dominated plots; however, we do not imply that forbs are inherently undesirable in our study system. We hypothesized that, relative to grass-dominated plots, disturbed plots as defined above would have:

- *Hypothesis 1a.* Higher soil fertility (nitrate, phosphorus, potassium), lower carbon-to-nitrogen ratio (C:N), less soil organic matter, and coarser soil texture
- *Hypothesis 1b.* Higher seedbank abundance, species richness, and Shannon-Wiener diversity

- *Hypothesis 1c.* More bare ground, lower litter accumulation, and higher forb cover in the aboveground vegetation
- *Hypothesis 1d.* Higher crude protein content and lower digestibility of the aboveground vegetation

In addition to this aboveground-driven approach, we also implemented a belowground-driven approach in which we did not make any *a priori* distinction between grass-dominated and disturbed plots. Instead, we studied associations between aboveground and belowground parameters across all available plots. We hypothesized that:

- *Hypothesis 2a.* Higher soil nitrate concentration and soil organic matter would correspond with a larger soil seedbank
- *Hypothesis 2b.* Higher soil organic matter and pH would correspond with more aboveground biomass
- *Hypothesis 2c.* Higher soil nitrate concentration would correspond with more nutritious and digestible plants aboveground

Methods

Ranch History

The study was performed in native tallgrass prairie at the Kansas State University Rannells Ranch near Manhattan, KS (39°08'33.9"N, 96°31'15.8"W). The 30-year normals (1991–2020) are 19.6°C for maximum annual temperature, 5.9°C for minimum annual temperature, and 82 cm for annual precipitation (NOAA NCEI, 2026).

The 11.8-km² ranch is divided into 25 paddocks used for continuous grazing of stocker cattle (yearling steers and/or heifers). Grazing systems used on the property include intensive early stocking (May to July), season-long stocking (May to October), and three-quarters stocking (May to August). The average annual stocking rate is approximately 2.5 animal unit–months per ha. Over the last two decades, prescribed fire has been implemented in late April across most of the property each year, with a few exceptions (2012, 2020, 2024). Prescribed fire was implemented in April 2025. Weeds and woody plants have been managed primarily with spot treatments of Group 4 herbicides such as 2,4-D and triclopyr. Other herbicides, such as imazapyr and glyphosate, have also been incorporated for weeds such as old-world bluestems (*Bothriochloa* spp.).

Plot Selection

Plots were identified in October 2024, at the end of the grazing season. This approach mimics a real-world scenario in which a producer might assess vegetation health upon removal of the livestock. A polygon shapefile of the 25 paddocks at Rannells Ranch was uploaded into QGIS (version 3.38; QGIS Development Team, 2024). Using the *Random Points Within Polygon* tool, one randomized marker was generated within each paddock. These randomized markers served as starting locations for selection of paired sampling plots representing native grass-dominated and disturbed vegetation.

To select sampling plots, we began at the nearest road-accessible point for each randomized marker. The two plots associated with each randomized marker were required to be no more than 450 m apart and located at least 10 m from roads and fencelines. The average distance between paired plots was 98 m with a range of 25 m to 442 m. Once each plot was selected, a 10 m by 10 m sampling area was established and coordinates were recorded.

Criteria used to identify grass-dominated and disturbed plots are listed in Table 1. Briefly, grass-dominated plots were defined as areas with high (>50%) cover of native warm-season grasses and few early-successional forbs. Species characteristic of grass-dominated areas included little bluestem [*Schizachyrium scoparium* (Michx.) Nash], big bluestem [*Andropogon gerardii* Vitman], Indiangrass [*Sorghastrum nutans* (L.) Nash], switchgrass [*Panicum virgatum* L.], sideoats grama [*Bouteloua curtipendula* (Michx.) Torr.], and blue grama [*Bouteloua gracilis* (Kunth) Lag. ex Griffiths]. Disturbed plots were defined as areas with bare soil, many early-successional forbs, and/or woody vegetation. Species characteristic of disturbed areas included smooth sumac [*Rhus glabra* L.], New Jersey tea [*Ceanothus americanus* L.], coralberry [*Symphoricarpos orbiculatus* Moench], western ragweed [*Ambrosia psilostachya* DC.], white sagebrush [*Artemisia ludoviciana* Nutt.], buffalobur [*Solanum rostratum* Dunal], Baldwin's ironweed [*Vernonia baldwinii* Torr.], common milkweed [*Asclepias syriaca* L.], tall goldenrod [*Solidago altissima* L.], and curlycup gumweed [*Grindelia squarrosa* (Pursh) Dunal].

Soil Nutrients

Soil samples were collected within a one-month period during October–November 2024 and again during May–June 2025. All disturbed (n = 25) and grass-dominated plots (n = 25) were sampled. One plot was lost, so the sample size is n = 49 plots per season. Composite samples were generated using a combination of 2.54 cm diameter and 3.81 cm diameter soil corers available. Within each 10 m by 10 m plot, 18 round soil cores (2.54 cm diameter, 10 cm depth) or 9 round soil cores (3.81 cm diameter, 10 cm depth) were collected in a grid pattern. All soil nutrient samples were submitted to the Kansas State University Soil Testing Laboratory for analysis (KSU Soil Testing Lab, 2026). The nutrients and properties analyzed included soil texture (percentage of sand, silt, and clay), pH and Sikora pH, total nitrogen, nitrate [NO₃⁻],

ammonium [NH₄⁺], total carbon, soil organic matter, phosphorus, potassium, calcium, magnesium, and sodium.

Soil Seedbank

Soil seedbank samples were collected concurrently with soil samples during October–November 2024 and again during May–June 2025. All disturbed plots were sampled for the soil seedbank (n = 25) while only a subset of grass-dominated plots were sampled (n = 10–11, in 2024 and 2025, respectively). Within each 10 m by 10 m plot, eighteen round soil cores (2.54 cm diameter, 10 cm depth) were collected in a grid pattern. All cores from a plot were mixed in a bucket. The homogenized sample was transferred to a labeled 1-gallon Ziploc® bag, stored in a cooler with ice packs in the field, and refrigerated at 4.4°C until processing.

To quantify the germinable soil seedbank, samples were removed from refrigeration and passed through a 9-mm sieve to remove large stones, roots, and coarse organic material while breaking up soil aggregates. The sieved soil was spread evenly over approximately 4 cm of potting mix (Berger BM6 Optimal Porosity potting mix; Berger International, Saint-Modeste, Québec, Canada) in germination trays and lightly incorporated into the upper 0.5 cm of the substrate. Trays were watered daily, and a water-soluble liquid fertilizer was applied biweekly (Miracle-Gro Water Soluble All Purpose Plant Food 24–8–16 NPK diluted by 0.5; Scotts Miracle-Gro, Marysville, Ohio, United States). Germination was monitored weekly, and all emerged seedlings were identified and recorded. Within the temperature-controlled greenhouse, conditions averaged 22.8°C nighttime temperature with 28.9% humidity and 28.3°C daytime temperature with 21.4% humidity. Only natural light passing through white-washed frosted glass was used to grow plants.

Aboveground Vegetation

Aboveground vegetation surveys were conducted over a one-week period in August 2025. These surveys were conducted in a subset of the paired plots ($n = 11$ grass-dominated plots and the corresponding $n = 11$ disturbed plots). In each sampled plot, four 0.5 m^2 quadrats were randomly placed. Data collected in the quadrats included the three most abundant (by cover) grass or graminoid species, the five most abundant forb species, percent grass cover, percent forb cover, percent litter (residue, thatch), percent bare ground, and average grass height.

Forage Quality

Forage biomass was collected in October 2024 and October 2025. The timing of forage collection was based on site access; forage samples were collected concurrently with initial soil and seedbank sampling. These samples were collected in the same set of plots used for aboveground vegetation surveys ($n = 22$). In each sampled plot, two 0.5 m^2 quadrats were randomly placed. All standing forage was clipped approximately 2.5 cm above the soil surface. Samples were oven-dried at 60°C for 48 hours, ground using a forage grinder to pass through a 2 mm screen (Wiley Mill, Thomas Scientific, Swedesboro, NJ, USA or Udy Cyclone Sample Mill, UDY Corporation, Fort Collins, CO, USA), and submitted for wet chemistry analysis at Dairy One Forage Testing Laboratory (Dairy One, Inc., Ithaca, New York, United States).

Statistical Analysis

Statistical analysis was conducted in R (version 4.4.1; R Core Team, 2024). To test for an association between plot type (grass-dominated vs. disturbed) and soil characteristics, we constructed linear mixed models (package “lme4”) with plot type, sampling time (fall vs. spring),

and the interaction as fixed effects. For soil texture (sand, silt, and clay), only fall data were used and sampling time was not included because we assumed that these parameters would not change between sampling times. Pasture (pair of grass-dominated and disturbed plots) was included as a random effect. To meet model assumptions, certain response variables were transformed as follows: $\text{NO}_3^{1/2}$, $\ln(\text{P})$, $\text{K}^{1/3}$, CN^{-4} , $\text{Clay}^{1/2}$. Significance was assessed by Type III ANOVA at $\alpha = 0.05$.

To test for associations between plot type and seedbank abundance or species richness, we constructed negative binomial generalized linear mixed models (log link) with plot type, sampling time, and the interaction as fixed effects and pasture as a random effect. For Shannon-Wiener diversity, this approach was not necessary and we instead used linear mixed models as described above for soil characteristics. Significance was assessed by Type III ANOVA and Tukey's HSD for post-hoc comparisons at $\alpha = 0.05$ (package "emmeans").

Aboveground vegetation cover was evaluated using the same approach described for soil characteristics, except that sampling time was not included because these data were only collected in 2025. A natural log transformation was applied to percent litter and a one-fourth power transformation was applied to percent forb. Forage quality was evaluated using the same approach described for soil characteristics. Square-root transformations were applied to crude protein and acid detergent fiber.

In addition to the analyses comparing disturbed with grass-dominated plots, we also used analysis of covariance to explore associations between soil characteristics, seedbank abundance, forage quality, and aboveground biomass. These additional analyses were performed across all

plots for which data were available. They were structured as generalized linear mixed models with the plant variables treated as response variables and soil variables treated as covariates.

For analyses linking soil variables with seedbank abundance (total abundance vs. nitrate or organic matter), we constructed negative binomial generalized linear mixed models (log link) with soil variables, sampling time (Fall 2024 vs. Spring 2025) and the interaction as predictors. Both the pasture and the unique individual plot were treated as random effects.

For analyses linking soil variables with biomass (biomass vs. pH or organic matter), predictors were the soil variable, sampling time (Fall 2024 vs. Spring/Fall 2025), and the interaction. Both the pasture and the unique individual plot were treated as random effects. For the biomass-vs.-organic matter model, biomass had a square root transformation. The analyses linking soil variables with forage quality (crude protein or acid detergent fiber vs. nitrate or organic matter), were carried out in the same way, except that the forage quality response was log-transformed. Predictors were the soil variable, sampling time (Fall 2024 vs. Spring/Fall 2025), and the interaction. Both the pasture and the unique individual plot were treated as random effects.

Results

Comparisons between Grass-Dominated and Disturbed Plots

Disturbed plots had higher nitrate, phosphorus, and potassium concentrations, C:N, and organic matter than grass-dominated plots ($P < 0.05$; Table 2). There was no difference in soil texture between grass-dominated and disturbed plots (Table 2). Nitrate and phosphorus concentrations also differed by sampling time ($P < 0.001$; Table 2). In both cases, these values

were higher in the spring after prescribed fire than in the fall. There was no interaction between plot type and sampling time.

Total seedbank abundance was higher in disturbed plots than grass-dominated plots ($P = 0.018$). As grass seedbank abundance did not differ between plot types ($P = 0.957$; Figure. 2.1A), the difference in total seedbank abundance was driven by a difference in forb seedbank abundance ($P = 0.002$; Figure. 2.1B). For the forb seedbank, there was also an interaction between plot type and sampling time ($P = 0.015$). The forb seedbank was larger in the fall for the disturbed plot type than for all other combinations of plot type and sampling time. Species richness of the total seedbank was higher in disturbed plots ($P = 0.027$) and in the fall ($P = 0.025$; Figure. 2.1C). Shannon-Wiener diversity of the total seedbank was higher in disturbed plots ($P = 0.019$) and in the fall ($P = 0.017$; Figure. 2.1D).

In the aboveground vegetation survey, percent bare ground, expressed as mean (standard error), was 27.4 (1.8) in disturbed plots and 31.2 (3.1) in grass-dominated plots ($P = 0.295$). Percent litter was 14.3 (3.1) in disturbed plots and 6.6 (1.8) in grass-dominated plots ($P = 0.034$). Percent forb cover was 27.0 (4.1) in disturbed plots and 26.8 (4.3) in grass-dominated plots ($P = 0.780$). Percent grass cover was 43.4 (5.5) in disturbed plots and 50.7 (6.6) in grass-dominated plots ($P = 0.352$).

Vegetation crude protein was higher in disturbed plots than grass-dominated plots ($P < 0.001$; Figure. 2.2A). In addition, crude protein was higher in Fall 2025 than Fall 2024 ($P < 0.001$). Amylase-treated Neutral Detergent Fiber was higher in Fall 2024 than Fall 2025 ($P < 0.001$) but did not vary by plot type ($P = 0.075$; Figure. 2.2B). Likewise, acid detergent fiber was

higher in Fall 2024 than Fall 2025 ($P < 0.001$) but did not vary by plot type ($P = 0.059$; Figure. 2.2C).

Analysis of Covariance Across All Plots

We used analysis of covariance to test whether soil factors explained any variability in seedbank or aboveground vegetation. For the seedbank, we found that total seedbank abundance was higher in Fall 2024 than Spring 2025 ($P = 0.006$) but was not affected by soil nitrate concentration ($P = 0.172$; Figure. 2.3A). However, when we tested soil organic matter as a covariate in a model of total seedbank abundance, we found that there was an interaction between organic matter and sampling time ($P = 0.041$) in addition to the main effect of sampling time ($P = 0.007$; Figure. 2.3B). In Fall 2024, total seedbank abundance was higher overall but tended to decline with increasing organic matter, whereas Spring 2025 total seedbank abundance tended to increase with increasing organic matter. There was no correlation between organic matter ($P = 0.800$) or sampling time ($P = 0.189$) and aboveground biomass. There was also no correlation between soil pH ($P = 0.135$) or sampling time ($P = 0.186$) and aboveground biomass.

Vegetation crude protein was higher in Fall 2025 than Fall 2024 ($P < 0.001$) but was not significantly associated with nitrate ($P = 0.052$; Figure. 2.4A). Likewise, crude protein was higher in Fall 2025 than Fall 2024 ($P = 0.032$) but was not significantly associated with organic matter ($P = 0.431$; Figure. 2.4B). Acid detergent fiber was higher in Fall 2024 than Fall 2025 ($P = 0.030$ or 0.031) but was not significantly associated with nitrate ($P = 0.370$; Figure. 2.4C) or organic matter ($P = 0.074$; Figure. 2.4D).

Discussion

This study demonstrated numerous connections between soil, seedbank, and forage characteristics across two years. For our main analysis, we mimicked producer surveys of aboveground vegetation at the end of the grazing season. As such, we used a binary classification separating areas with healthy native grass communities (“grass-dominated”) from areas in which these communities were replaced by early-successional forbs, woody species, and/or bare ground (“disturbed”). We found that this binary classification helped explain variation in soil fertility, seedbank abundance and diversity, aboveground plant litter, and crude protein.

The finding that disturbed plots had higher nitrate, phosphorus, and potassium levels than grass-dominated plots is consistent with *Hypothesis 1a*. This finding could reflect several processes, which may co-occur. The early-successional forbs found in most disturbed plots would exhibit strong responses to soil nutrient availability (Koerner et al., 2016; Zimdahl, 2018). Cattle dung and urine create patches of high nutrient availability, which affect plant growth (Sitters & Olde Venterink, 2021; Steinauer & Collins, 2001; Steiner et al., 2019) and, in the case of our study, might accelerate colonization by ruderal species. Another possible explanation for our finding is that the plants found in disturbed plots increased soil fertility. Disturbed plots included the following legume species: leadplant (*Amorpha canescens* Pursh), blue wild indigo [*Baptisia australis* (L.) R.Br.], purple prairie clover (*Dalea purpurea* Vent.), roundheaded lespedeza (*Lespedeza capitata* Michx.), violet bushclover [*Lespedeza violacea* (L.) Pers.], Nuttall’s sensitive briar [*Mimosa quadrivalvis* var. *nuttallii* (DC.) Beard ex Barneby], and wild alfalfa [*Pedimelum tenuiflorum* (Pursh) A.N.Egan]. Biological nitrogen fixation by these species would increase soil nitrate availability. Consistent with this interpretation, we observed

higher crude protein in disturbed plots (supporting *Hypothesis 1d*). Many tallgrass prairie forbs also have deep taproots, in comparison with the fibrous root systems of grasses. Forbs and woody plants can move nutrients, including less mobile nutrients such as phosphorus, up from deep in the soil profile (Gao et al., 2019; He & Li, 2016; Jobbágy & Jackson, 2001). This process could increase availability in the upper levels of the soil profile, where we sampled the soil. In addition, differences in soil nutrient availability could reflect faster nutrient turnover in early-successional forbs or highly efficient nutrient scavenging by native perennial grasses (Dubeux et al., 2007; Tilman & Wedin, 1991; Wedin & Tilman, 1993; Yahdjian et al., 2017).

Contrary to *Hypothesis 1a*, we observed higher C:N and higher soil organic matter in disturbed plots compared with grass plots. As noted above, it is possible that early-successional forbs and other species characteristic of disturbed plots might preferentially colonize more fertile soils. At the same time, high C:N in soils underlying disturbed plots could reflect the high C:N of woody shrubs (Acharya et al., 2020; De Deyn et al., 2008; Raven et al., 2004). These plant tissues are slow to degrade in soil (Taylor et al., 1989). Shrub encroachment has been both positively and negatively associated with increased topsoil soil organic carbon, although positive effects are more common (H. Li et al., 2016). For some of the measured parameters, especially soil organic matter, we also note that soil characteristics change more slowly than aboveground plant community composition (W. Li et al., 2018; Medina-Roldán et al., 2012; Poeplau et al., 2011). Although there was no difference in aboveground biomass at the time of our measurements, observed variation in soils might reflect the legacy of past variation in total productivity or in root-to-shoot ratios.

We observed twice as much litter cover in disturbed plots compared with grass-dominated plots, contradicting *Hypothesis 1c*. As biomass did not differ between disturbed and

grass-dominated plots, this difference might have reflected differences in species composition. Some species occupying disturbed plots, including woody species (e.g., smooth sumac, New Jersey tea, coralberry) and herbaceous species with defenses against herbivory (e.g., buffalobur, curlycup gumweed), would rarely be consumed by cattle. Low consumption could lead to more aboveground plant material, including persistent woody material, remaining as litter (Mapfumo et al., 2002; Medina-Roldán et al., 2012; Naeth et al., 1991). Another factor affecting litter persistence would be temperature and speed of prescribed fire as it travels across a patch of vegetation. Because fire behavior is strongly dependent on fuel bed characteristics (Wragg et al., 2018), it would differ between grass-dominated and disturbed plots.

Seedbank abundance, species richness, and Shannon-Wiener diversity were higher in disturbed plots than grass-dominated plots. This finding is consistent with *Hypothesis 1b*. It likely reflects the fact that disturbed plots contained more early-successional species, which tend to be more reliant on abundant and persistent seedbanks (Kelemen et al., 2017; Thompson et al., 1998). However, the substantial difference between fall and spring seedbanks did suggest that species with more transient seedbanks represented a major component of the entire community-level seedbank. Interestingly, the observed response of seedbank abundance to the interaction between organic matter and sampling time represented the only significant result from our analyses of covariance (*Hypotheses 2a, 2b, 2c*). This significant interaction may reflect seasonal turnover in species composition of the soil seedbank, consistent with the idea that the seedbank has a substantial transient component (Csontos, 2007; Peng et al., 2025; Walck et al., 2005). If the fall vs. spring seedbanks are dominated by different species, these different species may show different responses to soil organic matter or correlated edaphic variables (e.g., differences

in seed production, seed germination, and seed mortality), resulting in different levels of seedbank abundance.

Implications

This study demonstrates that end-of-season visual assessments of aboveground vegetation can provide substantial insight into soil fertility, soil seedbanks, and forage quality, even in the absence of quantitative measurements. Although not tested in our study, in-season assessments would likely provide similar insight.

Although limited in detail, visual assessments play an important role in helping range managers identify priority areas for management. In our study, we contrasted this visual-assessment approach with quantitative analyses of covariance that avoided *a priori* categorization of rangeland areas. In our study, the analyses of covariance proved less successful in demonstrating associations between aboveground and belowground parameters. The fundamental reason for this outcome was that the visual “grass-dominated vs. disturbed” classification essentially integrated multiple relevant differences between rangeland areas into a categorical predictor, whereas each analysis of covariance relied on a single quantitative predictor.

The key takeaway from our research is not that visual assessments alone are sufficient to understand ecosystem dynamics. In fact, our research demonstrated significant shortcomings of end-of-season visual assessments, including a limited ability to predict aboveground vegetation characteristics for the subsequent grazing season. Nevertheless, we interpret our findings to mean that the qualitative information already being gathered by land managers provides important

clues about ecological processes that are much more difficult to track. Continued advances in decision support can help managers make the best possible use of this information.

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Tables

Table 1.Criteria used to define and select “grass-dominated” and “disturbed” plots.

Grass-dominated plots	Disturbed plots
A) Native warm-season grasses AND	A) Woody/shrubby vegetation AND/OR
B) Fewer early-successional forbs	B) Many early-successional forbs AND/OR
	C) Weeds present in addition to lots of bare soil indicating recent disturbance

Table 2. Associations between plot type (disturbed vs. grass-dominated), sampling time (fall vs. spring), and soil characteristics. Raw data are shown but statistical analyses were performed on transformed scales.

Plot by time	NO ₃ (ppm)	P (ppm)	K (ppm)	C:N	Organic matter (%)	Clay (%)	Silt (%)	Sand (%)
Disturbed Fall	2.4 (0.3)	3.2 (0.3)	411.2 (22.4)	13.4 (0.3)	7.0 (0.2)	21.4 (1.8)	59.0 (1.5)	19.7 (1.0)
Disturbed Spring	5.3 (0.7)	5.0 (0.6)	430.3 (29.7)	13.4 (0.3)	7.4 (0.2)	—	—	—
Grass Fall	1.4 (0.2)	1.8 (0.1)	334.0 (16.1)	13.9 (0.4)	6.8 (0.2)	18.6 (1.5)	60.6 (1.2)	20.8 (1.1)
Grass Spring	4.1 (0.4)	2.8 (0.3)	329.3 (16.3)	14.0 (0.3)	6.8 (0.2)	—	—	—
P values								
Plot type	<0.001	<0.001	<0.001	0.003	0.010	0.082	0.345	0.071
Sampling time	<0.001	<0.001	0.813	0.844	0.268	—	—	—
Interaction	0.627	0.989	0.508	0.509	0.268	—	—	—

Figures

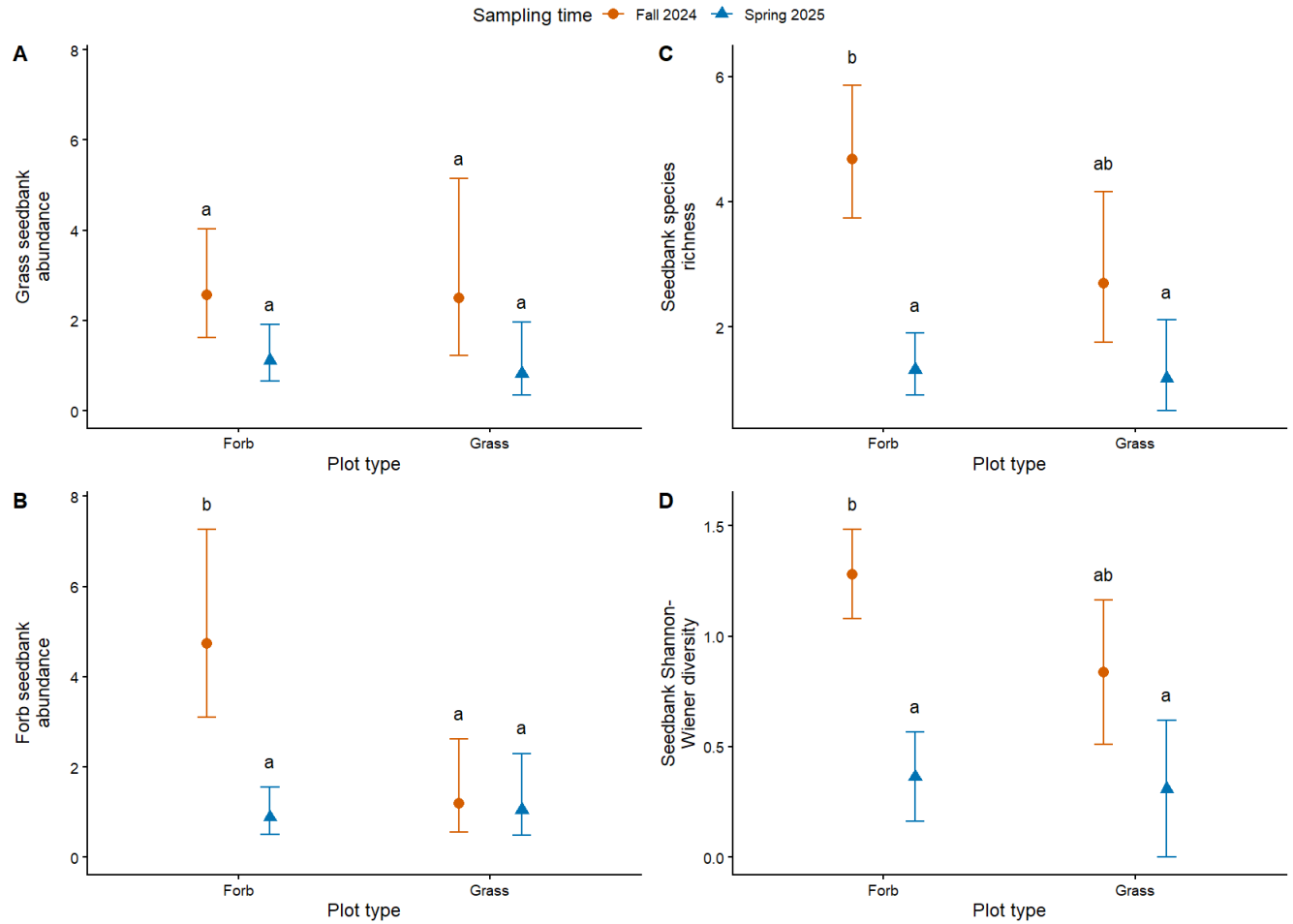


Figure 2.1. Associations between plot type (disturbed vs. grass-dominated), sampling time (Fall 2024 vs. Spring 2025), and seedbank characteristics (abundance of grass seeds, abundance of forb seeds, species richness, Shannon-Wiener diversity). Estimated marginal means are shown with 95% confidence intervals. For abundance and species richness, estimated marginal means are back-transformed from the log scale on which analyses were performed. Different letters indicate significant differences according to Tukey's HSD at $\alpha = 0.05$. The seedbank was evaluated using 0.9 L soil per plot.

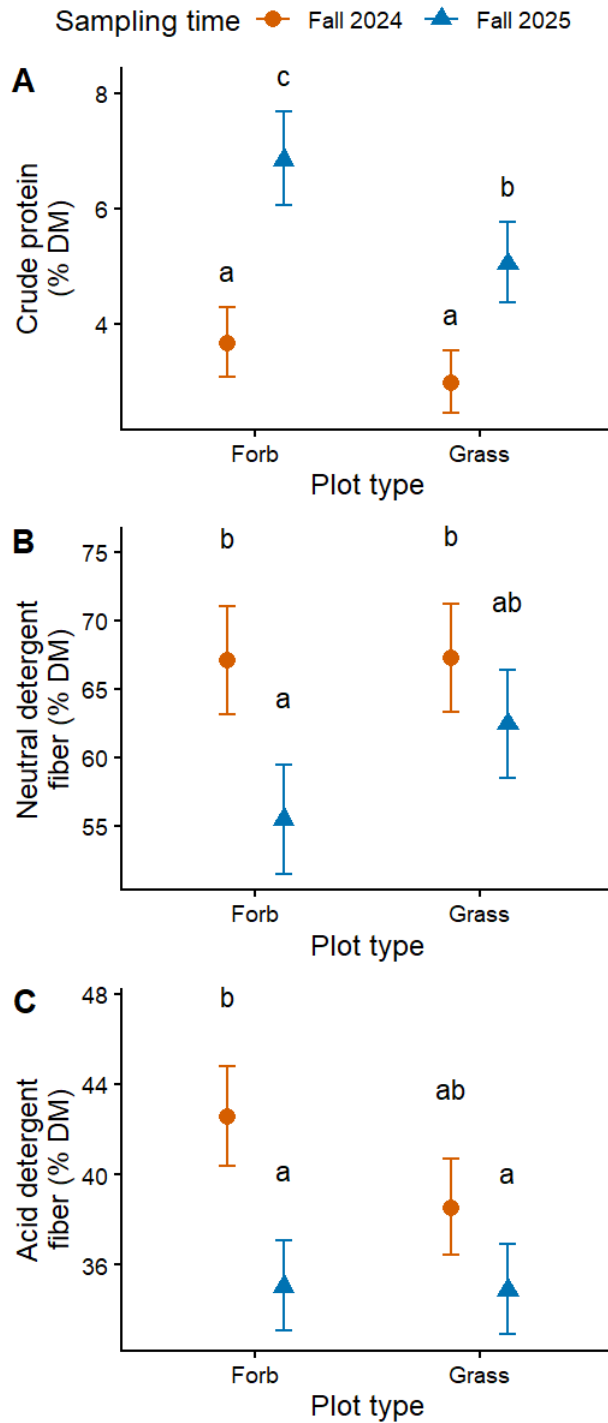


Figure 2.2. Associations between plot type (disturbed vs. grass-dominated), sampling time (Fall 2024 vs. Fall 2025), and forage quality characteristics. Estimated marginal means are shown with 95% confidence intervals. For crude protein and acid detergent fiber, estimated marginal means are back-transformed from the square root scale on which analyses were performed. Different letters indicate significant differences according to Tukey’s HSD at $\alpha = 0.05$.

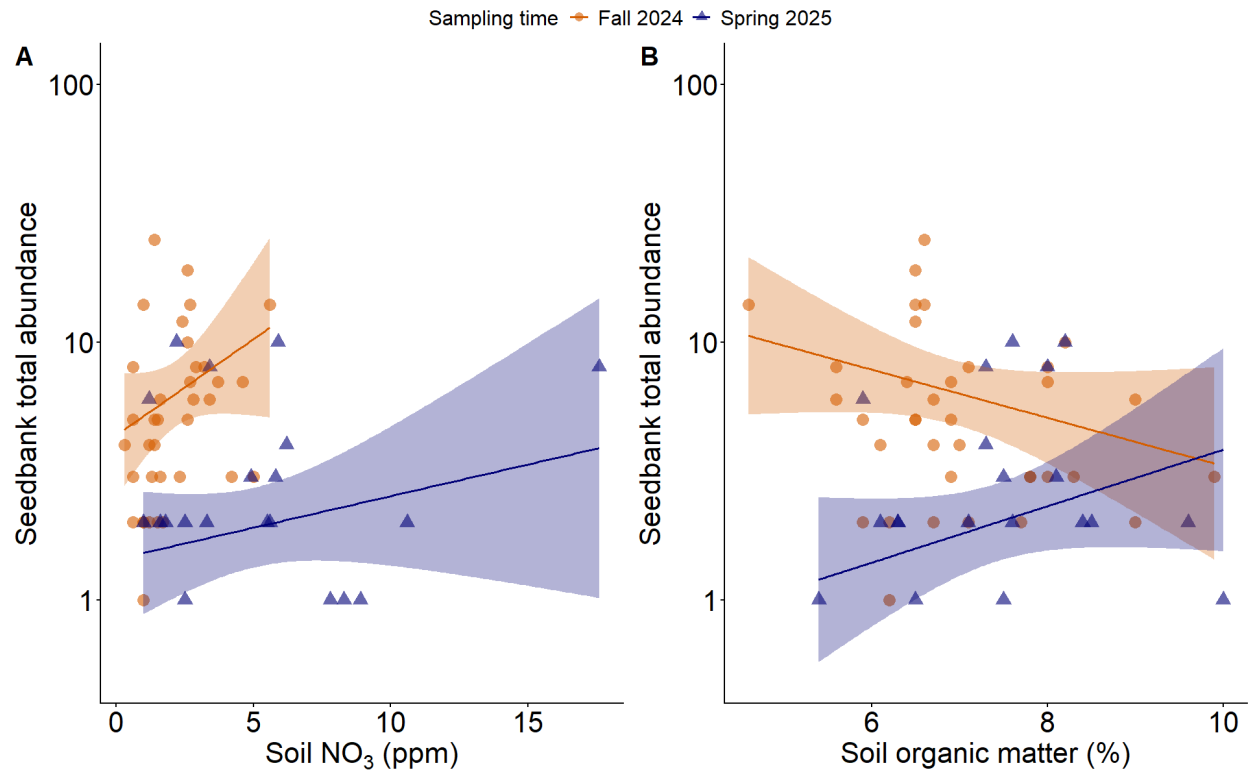


Figure 2.3. Correlations of soil nitrate (A) or soil organic matter (B) with total seedbank abundance. Points represent raw data. Lines represent back-transformed predictions from the models described in the text. Ribbons represent 95% confidence intervals. The y-axis is shown on a logarithmic scale. The seedbank was evaluated using 0.9 L soil per plot.

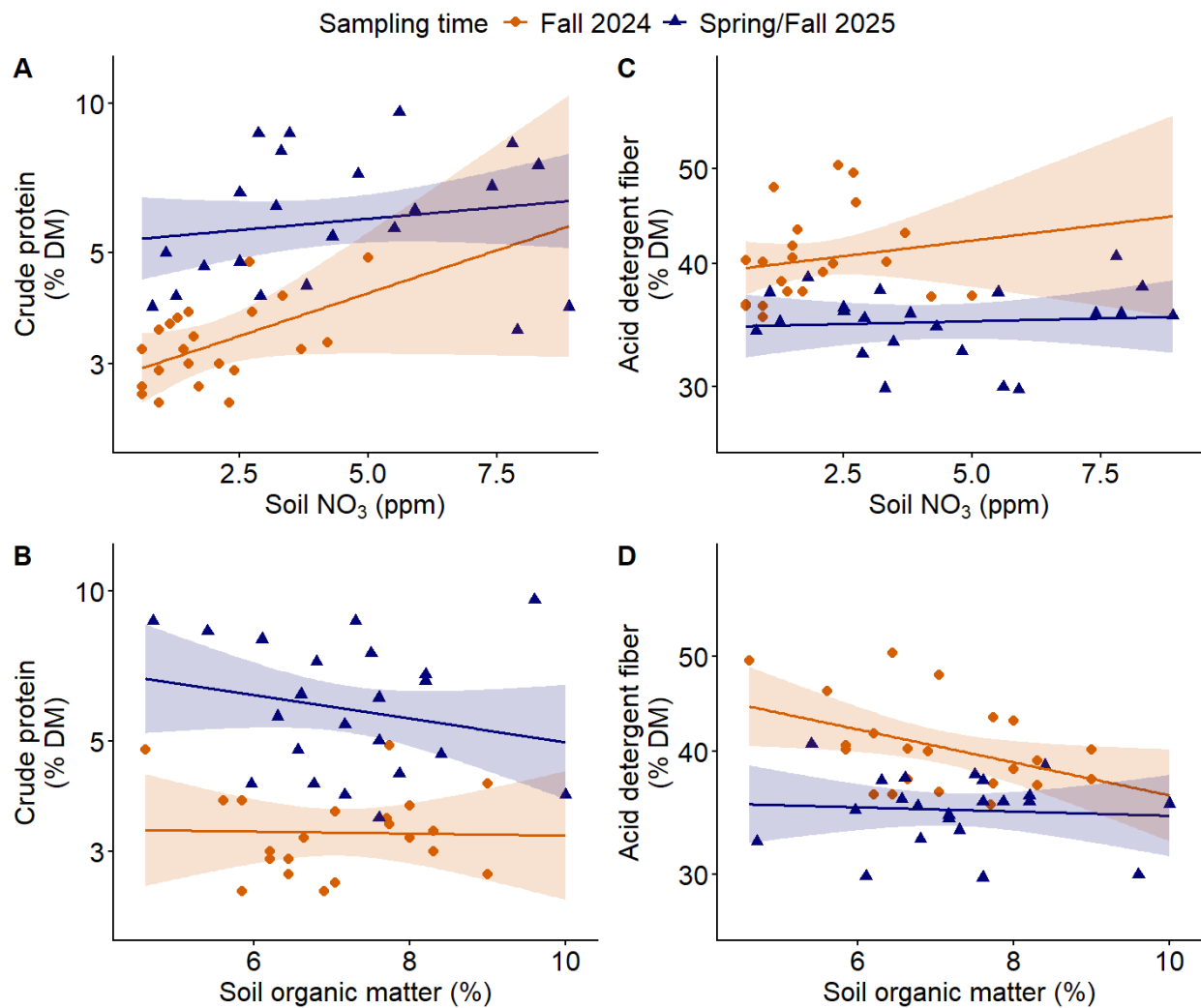


Figure 2.4. Correlations of soil nitrate (A, C) or soil organic matter (B, D) with crude protein (A, B) or acid detergent fiber (C, D). Points represent raw data. Lines represent back-transformed predictions from the models described in the text. Ribbons represent 95% confidence intervals. The y-axis is shown on a logarithmic scale.

Chapter 3

Effects of UAV-applied triclopyr plus fluroxypyr rates on weeds and desirable forbs in Kansas tallgrass prairie

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Abbreviations: DAT, days after herbicide treatment; NDVI, Normalized Difference Vegetation Index; UAV, Uncrewed Aerial Vehicle; WSP, water-sensitive papers

Abstract

We studied the impacts of UAV-applied triclopyr + fluroxypyr on rangeland weeds and other forbs in native tallgrass prairie. Two rates were tested: high (0.63 kg ae ha⁻¹ triclopyr + 0.21 kg ae ha⁻¹ fluroxypyr) and low (0.21 kg ae ha⁻¹ triclopyr + 0.07 kg ae ha⁻¹ fluroxypyr). We evaluated injury to established plants [Baldwin's ironweed (*Vernonia baldwinii* Torr.), goldenrod (*Solidago spp.*), leadplant (*Amorpha canescens* Pursh), western ragweed (*Ambrosia psilostachya* DC.), and white sagebrush (*Artemisia ludoviciana* Nutt.)] and potted seedlings [alyssum (*Lobularia maritima* (L.) Desv.), Baldwin's ironweed, common evening primrose (*Oenothera biennis* L.), common milkweed (*Asclepias syriaca* L.), and sericea lespedeza (*Lespedeza cuneata* (Dum. Cours.) G. Don)]. For established plants, herbicide treatments did not impact percentage cover of individual species, although they did reduce total forb cover ($P = 0.04$). The high herbicide rate increased visual injury in all species ($P < 0.05$). For seedlings, visual injury was observed at both herbicide rates for Baldwin's ironweed, common milkweed, and sericea lespedeza ($P < 0.01$). Water-sensitive papers revealed low and variable levels of spray coverage with apparent drift onto control plots. Percentage change in Normalized Difference Vegetation Index (NDVI) over time was positive in the control treatment, slightly negative at the low herbicide rate, and more negative at the high herbicide rate ($P < 0.001$). Advances in UAV technology will continue to promote spraying and sensing applications in rangeland environments, although the potential for non-target impacts should be incorporated into management guidance.

Introduction

Herbicides are a crucial method for rangeland weed management (DiTomaso, 2000; DiTomaso et al., 2010; Young et al., 2025). In rangeland environments, Uncrewed Aerial Vehicles (UAVs) can facilitate herbicide applications in areas that are difficult to access with ground-based equipment. However, these aerial applications can also come with drawbacks. Rangeland herbicide applications in general may lead to non-target impacts on desirable native plants and secondary invasions (Ortega & Pearson, 2011; Rinella et al., 2009). UAVs potentially exacerbate these problems due to the greater potential for drift when herbicides are applied aerially, compared with ground-based applications (Butts et al., 2022; P. Chen et al., 2022; X. Chen et al., 2025). In addition to applying herbicides, UAVs also have the potential to help monitor herbicide efficacy and non-target impacts. This potential has previously been demonstrated primarily in crop environments (Abrantes et al., 2021; Duddu et al., 2019; Huang et al., 2018; Mink et al., 2020). In a previous rangeland study, UAV imagery was used to measure canopy change after herbicide treatment (Shen et al., 2023).

Group 4 herbicides mimic the natural plant hormone auxin, thereby disrupting plant growth. These herbicides are frequently used to control broadleaf and woody plants in rangeland environments (Lancaster et al., 2026; MacDonald et al., 2013). In many cases, they are also eligible for cost-share under state noxious weed programs. For instance, in Kansas rangelands, the combination of triclopyr and fluroxypyr is recommended for control of sericea lespedeza [*Lespedeza cuneata* (Dum. Cours.) G. Don] (Kansas Department of Agriculture, 2022; Lancaster et al., 2026). Sericea lespedeza is economically and environmentally harmful and difficult to control (Barnes et al., 2022; Pile Knapp et al., 2025; Sherrill et al., 2022).

Multiple studies have demonstrated the potential for non-target effects of triclopyr and fluroxypyr. A study in Illinois tested five treatments of triclopyr or triclopyr plus fluroxypyr for control of sericea lespedeza (Gibson et al., 2019). The herbicide treatments reduced stem density of sericea lespedeza without compromising taxonomic diversity. However, the herbicide treatments increased the net relatedness index, indicating reduced phylogenetic diversity (Gibson et al., 2019). Multivariate tests also demonstrated impacts of herbicide treatments on species composition (Gibson et al., 2019). A dose-response field study in Colorado applied multiple rates of triclopyr (up to 3.92 kg ai ha⁻¹, twice the typical field application rate) to desirable restoration species (Douglass et al., 2016). The authors observed triclopyr sensitivity in American licorice (*Glycyrrhiza lepidota* Pursh) and to a lesser extent in alkali sacaton [*Sporobolus airoides* (Torr.) Torr.], sideoats grama [*Bouteloua curtipendula* (Michx.) Torr.], Canada wildrye (*Elymus canadensis* L.), and western wheatgrass [*Pascopyrum smithii* (Rydb.) A. Love]. There was no measurable response in fourwing saltbush [*Atriplex canescens* (Pursh) Nutt.], bottlebrush squirreltail [*Elymus elymoides* (Raf.) Swezey], or slender wheatgrass [*Elymus trachycaulus* (Link) Gould ex Shinner] (Douglass et al., 2016). A combination of triclopyr and fluroxypyr reduced plant species richness in Irish grasslands, regardless of whether the herbicide was broadcast, manually spot-sprayed, or spot-sprayed using an automated method (Power et al., 2013). In some cases, this herbicide mixture also reduced forb species richness or species diversity (Power et al., 2013). Non-target impacts can also occur when triclopyr is transported to non-target plants by flooding (Oberweiger et al., 2024). However, non-target impacts do not always occur at significant rates, and herbicides like triclopyr and fluroxypyr can also enhance native plant communities by removing weeds (Getsinger et al., 1997; Voinorosky & Stewart, 2021).

This study evaluates the impacts of triclopyr plus fluroxypyr on forbs in Kansas tallgrass prairie. The forbs addressed included sericea lespedeza, western ragweed (*Ambrosia psilostachya* DC.), leadplant (*Amorpha canescens* Pursh), white sagebrush (*Artemisia ludoviciana* Nutt.), common milkweed (*Asclepias syriaca* L.), alyssum [*Lobularia maritima* (L.) Desv.], common evening primrose (*Oenothera biennis* L.), goldenrod species (*Solidago spp.*), and Baldwin's ironweed (*Vernonia baldwinii* Torr.). In Kansas rangelands, these forbs exist along a spectrum of weediness. Sericea lespedeza is a legally designated noxious weed (Kansas Department of Agriculture, 2022) known for its high competitiveness and high tannin concentrations, making it undesirable as forage (Cummings & Bidwell, n.d.). In contrast, early-successional native forbs such as western ragweed can be locally problematic especially in disturbed areas, yet can be grazed in small quantities by cattle and provide forage and habitat for wildlife (Harmony et al., 2024). Other native species are frequently recognized for their ecological benefits; for instance, common milkweed serves as a larval host for monarch butterflies (*Danaus plexippus* L.) and a nectar source for other pollinators (Stup et al., 2025).

We tested the following five hypotheses:

- 1) All species, including both weedy and desirable forbs, will show symptoms of herbicide injury at 14 and 21 days after herbicide treatment (DAT).
- 2) First-year seedlings will be similarly vulnerable to high (recommended) and low (reduced) herbicide rates, whereas plants established in the field will tolerate the low rate.
- 3) Faster-growing weed species will show more tolerance to the low herbicide rate compared with other forbs.
- 4) Water-sensitive papers (WSP) show evidence of herbicide drift onto unsprayed areas.

- 5) The Normalized Difference Vegetation Index (NDVI), derived from UAV imagery, will distinguish between the high herbicide rate, low herbicide rate, and control.

Methods

Experimental Design and Treatments

The study was performed in native tallgrass prairie near Manhattan, Kansas (39.14 N, 96.54 W). The site is grazed by yearling steers under an intensive early stocking system (May to July, approximately 1 Animal Unit Month per 0.4 ha with ~2 Animal Units per ha). The study was repeated in time within the 2025 growing season with the two runs separated by a period of two weeks. The two runs took place in adjacent areas.

For each run of the experiment, twelve georeferenced plots (9.14 m by 30.48 m) were designated with a buffer zone of 9.14 m between plots (Figure 3.1). The twelve plots were arranged into four blocks. Within each block, the three plots were randomly assigned to three triclopyr + fluroxypyr rates (PastureGard® HL, Corteva Agriscience, Indianapolis, IN). The “high” rate was the recommended rate: 0.63 kg ae ha⁻¹ triclopyr + 0.21 kg ae ha⁻¹ fluroxypyr. The “low” rate was a reduced rate: 0.21 kg ae ha⁻¹ triclopyr + 0.067 kg ae ha⁻¹ fluroxypyr. A non-treated control was included for comparison. For both high and low herbicide rates, the application also included 0.47 L ha⁻¹ Superb® HC (crop oil concentrate, WinField® United, Minneapolis, MN) and 0.15 L ha⁻¹ InterLock® (drift reduction, WinField® United, Minneapolis, MN). The total application volume for both herbicide rates was 5 L ha⁻¹, in line with the standard practice of the applicator when spraying by UAV. The UAV was a DJI Agras T40 (DJI, Shenzhen, Guangdong Province, China). It had a coaxial twin-rotor design with improved lift efficiency and stability. The spray swath width was ~8.5 m, and the spray height was 3 m. Run 1

was sprayed on July 3, 2025 from 9:45am to 10:30am. Wind was 9.3 to 9.7 kph from the south to southwest. Relative humidity was 60.3% to 66.7% and air temperature was 27.6 to 29.3 C (Kansas State University, 2025). Cloud conditions were observed to be clear. Run 2 was sprayed on July 14, 2025 from 9:30am to 10:15am. Wind was 2.7 to 3.5 kph from the east to southeast. Relative humidity was 54.8% to 63.6% and air temperature was 27.1 to 29.3 C (Kansas State University, 2025). Cloud conditions were observed to be few clouds.

Plant Measurements

We measured the effects of herbicides on two sets of plants: mature, established plants that were already present in the field, and potted seedlings that we placed in the field prior to the herbicide application.

Mature plant species were leadplant, western ragweed, Baldwin's ironweed, white sagebrush, and goldenrod spp. These species are all native but vary in ecological function and desirability to cattle producers. For the mature plants, measurements were taken at 0 (pre-application), 7, 14, and 21 DAT. These measurements were taken within four 0.25 m² fixed quadrats per plot. The quadrats were placed every 6.1 m along the long axis of the plot, centered in terms of the short axis. Each week, we measured total forb cover and species-level cover for the five species of interest within each quadrat. Herbicide visual injury was measured on a scale of 1 to 10 for the five species of interest (Table 3).

For the potted seedlings, the five species were sericea lespedeza, common milkweed, albyssum, common evening primrose, and Baldwin's ironweed. Seeds were collected from nearby rangeland and roadside environments in 2024. Seeds received wet-cold stratification at 4 C prior to planting. For sericea lespedeza, which has physical dormancy, seeds were scarified with

sandpaper and, in Run 1, some seedlings previously germinated in a growth chamber were also added. Seeds were planted in 10-cm pots with Berger BM6 Optimal Porosity potting mix (Berger International, Saint-Modeste, Québec, Canada). The number of seeds per pot was 3, except for sericea lespedeza (3 to 5) and Baldwin's ironweed (4). Pots were randomly assigned to herbicide treatments and blocks at the time of seeding. At 4 weeks after seeding, we transplanted some seedlings from pots with multiple seedlings to pots without seedlings. Despite this transplanting, due to variable germination rates, actual sample sizes varied by combination of species, treatment, and run (Table 4).

The pots were grown in the greenhouse for six weeks before being transferred outdoors. They were kept outdoors under a polyethylene shade cloth providing 50% shade (Figure 3.2) for a three-day acclimation period prior to herbicide application. On the day of the herbicide application, pots were transferred into the field and placed in the center of their respective plots. Five hours after application, the trays were moved back under the 50% shade cloth structure for the 21-day monitoring period.

Potted plants were watered daily to field capacity throughout the study, including the period in the greenhouse, the acclimation period prior to herbicide application, and the monitoring period after herbicide application. Herbicide visual injury in the potted seedlings was measured on a 1 to 10 scale at 7, 14, and 21 DAT (Table 3).

WSP and UAV Imaging

The spray efficiency was measured using water sensitive paper (WSP) (SpotOn® WSP, 25.4 by 76.2 mm). Four WSP were placed in the center of each plot on the top leaf. WSP were collected within hours after application to avoid contamination from atmospheric moisture while

remaining compliant with the restricted entry interval for the herbicide. While collecting, each WSP was properly labelled on the back to identify treatment and replication. Following the collection, an image of each WSP was taken using an iPhone 17, and the images were processed using the open source software ImageJ (Hartig, 2013; Newton Martin et al., 2020). In ImageJ, images were scaled, cropped to isolate the target area, converted to 8-bit grayscale, and thresholded to enable coverage detection for all the pictures. Processed images were subsequently analyzed using Python (Python Software Foundation, 2023), employing libraries such as Pillow, NumPy, and OpenCV to convert those images into numerical matrices and quantify the number of pixels corresponding to spray coverage. Coverage percentage was calculated as the ratio of covered pixels to the total number of pixels per image.

In addition to WSP, high-resolution UAV images were collected on July 3, 2025 (pre-application for Run 1), July 14 (post-application for Run 1 and pre-application for Run 2), and July 29 (post-application for Run 2). Images were acquired using a DJI Mavic 3 Enterprise quadcopter with a multispectral sensor with four bands (Red, Green, Red-Edge, Near Infrared). UAV flight was implemented using DJI Pilot 2 software, with a flight height of 30 m, a spatial resolution of 3 by 3 cm per pixel, and side and front overlap of 80%. For radiometric calibration, a calibrated reflectance panel was used before and after each flight. Following image acquisition, post-processing was performed, with individual images stitched and georeferenced to generate high-resolution orthomosaic images using Pix4D software (Pix4D SA, 2023). The generated orthomosaic images were used to generate a normalized difference vegetation index (NDVI) map using the equation below, and the mean NDVI for each plot was then aggregated in QGIS software (QGIS Development Team, 2024).

$$NDVI = \frac{NIR - Red}{NIR + Red} \quad (1)$$

Statistical Analysis

All statistical analyses were conducted in R (version 4.4.1; R Core Team, 2024). For the analyses of mature plants, data were analyzed with linear mixed models (package “lme4”). Time (0, 7, 14, or 21 DAT), treatment (high herbicide rate, low herbicide rate, or control), and the interaction between time and treatment were treated as fixed effects. Run, plot, and fixed quadrat within the plot were treated as random effects. Significance was assessed by Type 3 ANOVA. Post-hoc comparisons were carried out using estimated marginal means and the Tukey method for p-value adjustment (package “emmeans”). To meet model assumptions of normality and homoskedasticity of residuals, transformations were applied as follows: square root for total forb cover, Baldwin’s ironweed injury, goldenrod injury, white sagebrush injury; one-fourth power for leadplant injury; log for Baldwin’s ironweed cover, goldenrod cover, leadplant cover, white sagebrush cover, western ragweed cover, and western ragweed injury. For potted seedlings, the approach was similar, except that fixed quadrat was not needed as a random effect. A fourth-power transformation was applied to injury for each species, except common milkweed for which no transformation was needed. For WSP, the log of percentage cover was analyzed in terms of treatment (fixed effect) and plot (random effect). For NDVI, percentage change (pre-herbicide to post-herbicide) was analyzed in terms of treatment (fixed effect) and run (random effect). Significance was assessed by Type 2 ANOVA. Post-hoc comparisons were carried out using estimated marginal means and the Tukey method for p-value adjustment ($\alpha = 0.05$).

Results and Discussion

Herbicide Impacts On Mature In-Field Plants

Total forb cover was influenced by time and the interaction between time and treatment (Table 5). Total forb cover showed only a slight decline over time in the control treatment (33% at 7 DAT to 26% at 21 DAT), compared with greater declines with the low herbicide rate (32% at 0 DAT to 20% at 21 DAT) or high herbicide rate (32% at 0 DAT to 18% at 21 DAT). Cover also decreased over time for leadplant (7% at 0 days to 5% at 21 days) and white sagebrush (5% at 0 DAT to 3% at 14 DAT). No other significant effects of time or treatment were observed (Table 3). These findings suggest that herbicide treatments did reduce forb cover but the effect only became significant when aggregated across multiple forb species.

Time affected visual injury scores for all species except white sagebrush (Table 5; Figure 3.3). In all species, some injury was observed prior to herbicide application because the injury scale was based on symptomology rather than causation (Table 3). For example, chlorosis was considered in the scoring and this symptom could have multiple causes unrelated to herbicides (e.g., pests, environmental stress). Drought could have contributed to observed increases in injury over time, independently of the herbicide application. On July 1st, prior to the start of our study, only 58.75% of the county was within a D0 (Abnormally Dry) drought zone (U.S. Drought Monitor, 2025). By August 5th, just after the study's end, 99.11% of the county was within a D0 drought zone (U.S. Drought Monitor, 2025). Our study site was within the drought zone between July 30 and August 5. A previous study from the same county demonstrated that drought conditions had more negative effects on goldenrod compared with the dominant native grass (Hoover et al., 2014).

Interactions between time and treatment affected visual injury scores for all species (Table 5; Figure 3.3). At the high rate, Baldwin's ironweed injury was highest at 14 DAT and lowest at 0 DAT (Figure 3.3). In the control, Baldwin's ironweed injury was higher at 7 DAT than 0 and 14 DAT. At the high rate, goldenrod injury was higher at 7 and 14 DAT than 21 and 0 DAT. In the control, goldenrod injury was highest at 7 DAT and lowest at 0 DAT. There was no significant change over time at the low rate in Baldwin's ironweed or goldenrod. For leadplant, injury at the high rate was greatest at 7 DAT, intermediate at 14 and 21 DAT, and lowest at 0 DAT. For western ragweed, injury at the high rate was lowest at 0 DAT. For white sagebrush, injury at the high rate was greater at 7 DAT than 0 DAT. There was no significant change over time at the low rate or in the control for leadplant, western ragweed, or white sagebrush (Figure 3.3).

These findings support our first hypothesis that all species would be affected by herbicide treatment, although we saw injury scores peaking at 7 DAT rather than the hypothesized 14 or 21 DAT. Effective control of several rangeland weeds is consistent with the product label, which specifically mentions control of ironweed and ragweed species (Corteva Agriscience, 2023). The high rate tested in our study is the highest legal rate (Corteva Agriscience, 2023). As predicted by Hypothesis 2, mature field plants were largely unaffected by the low herbicide rate, which is lower than the recommended range for control of established biennial and perennial forbs (Corteva Agriscience, 2023). In contrast with Hypothesis 3, we did not observe a difference between the responses of disturbance-adapted early-successional weed species, such as western ragweed and white sagebrush, and other species. Similarly, Power et al. (2013) found that triclopyr plus fluroxypyr could suppress both non-target plants and target weeds, although some application methods only suppressed non-target plants (Power et al., 2013).

Herbicide Impacts On Potted Seedlings

Among potted seedlings, time had a significant impact on visual injury ratings for all species (Table 6). In each of the five species tested, visual injury ratings were greater at 14 and 21 DAT than 7 DAT (no 0 DAT data were collected for potted seedlings). The increase in visual injury likely reflected the transition from the controlled greenhouse environment to a harsher field environment, which can be difficult for potted seedlings even with shade cloth and daily watering.

Treatment impacted visual injury ratings for Baldwin's ironweed, common milkweed, and sericea lespedeza. In each of these three species, visual injury was greater in the low-rate and high-rate treatments than the control (Figure 3.4). There were no significant differences between the low and high herbicide rates or interactions between herbicide treatment and time. For the species that were not impacted by herbicides, it is possible that the small potted seedlings were not hit by many herbicide droplets. The WSP showed low spray coverage (described below), which may be associated with the lower-than-recommended total application volume (Corteva Agriscience, 2023). In addition, the pots containing forb seedlings were placed on the ground in a grassland, so taller native grasses may have shielded the seedlings from much of the spray.

These findings partially support our first hypothesis that the herbicide treatments would injure all species. However, alyssum and common evening primrose were not significantly impacted by the herbicides. The second hypothesis was fully supported, as there was never a difference between the two herbicide rates for the potted seedlings. Less established plants are sometimes more susceptible to lower herbicide rates. Tomkins and Grant (1974) observed that weeds newly establishing in a disturbed area were more susceptible to herbicides than well-established weeds growing from rhizomes and stolons in a mature community. In another study,

low and high rates of nine herbicides, including triclopyr, were applied to seedlings of 10 species (Kaeser & Kirkman, 2010). Each species was tested at multiple growth stages: pre-emergent, 30 days after emergence, and 60 days after emergence. Herbicide sensitivity was often greater in younger plants (Kaeser & Kirkman, 2010). Our last hypothesis was not supported, as weediness again did not predict herbicide tolerance. However, we note that the noxious weed sericea lespedeza was controlled. This finding is consistent with the PastureGard label (Corteva Agriscience, 2023). Our high rate is the recommended rate for established sericea lespedeza plants, whereas lower rates can be used for young plants.

WSP and NDVI

Treatment affected percentage cover of the WSP ($P < 0.001$). Percentage cover was lower for the control (0.4 ± 0.1) than the low (3.1 ± 0.7) and high (3.2 ± 0.8) herbicide rates. These low levels of cover could have reflected a low total application volume and shielding by other plants. We observed significant variability in percentage cover among cards, which is not uncommon (Salyani & Fox, 1999). The two herbicide rates did not significantly differ in percentage cover of the WSP, which was expected because the total application volume was the same. Consistent with our fourth hypothesis, we did observe some spotting on the WSP even in the control treatment. As there was no rain during the short period that the WSP were in the field, this finding likely reflects herbicide drift.

Percentage change in NDVI (pre-application to post-application) was influenced by treatment ($P < 0.001$). Each of the three treatments differed from both the others. Percentage change in NDVI was positive in the control treatment ($0.4\% \pm 1\%$), slightly negative at the low herbicide rate ($-2.4\% \pm 1\%$), and more negative at the high herbicide rate ($-5.7\% \pm 1\%$). This

finding indicates that herbicide treatments reduced greenness of the plots, consistent with our fifth hypothesis. In Texas, NDVI has been used to create brush classification maps, enabling authors to measure herbicide efficacy as a change in canopy cover (Shen et al., 2023). In Wyoming, satellite-derived NDVI data have been used to track impacts of invasive weed control tactics, including herbicide applications (Johnston et al., 2018; Mattilio et al., 2025).

Practical Applications

In our study, we observed variable rates of herbicide injury, especially among the potted seedlings. These findings were apparently linked with low rates of spray coverage, suggesting that a greater total application volume might have yielded more uniform control. This practice would be recommended to ensure efficacy against weeds. However, increased coverage would also increase harm to non-target plants (Smith et al., 2023). As herbicide sensitivity did not differ between weedier and more desirable plants, it would be difficult to achieve selectivity by rate reductions. Instead, it may be better to focus on minimizing the sprayed area. Aerial imagery can be used for weed mapping to guide herbicide applications (Lehmann et al., 2017; Malmstrom et al., 2017; Pöttker et al., 2023), making it easier to avoid unnecessarily spraying areas without the target weeds. In some cases, an integrated UAV system can be used for both detection and spraying (Hunter et al., 2020).

All herbicide applications carry the potential for drift, but this potential can be greater with aerial application methods (Butts et al., 2022; P. Chen et al., 2022; X. Chen et al., 2025). In our study, WSP indicated that drift may have occurred across the 9 m buffer between plots. This drift potential can be problematic because young plants may be affected by herbicide concentrations much lower than the recommended application rate (Bolwerk et al., 2024; Marrs

et al., 1991; Wagner & Nelson, 2014). Consistent with this literature, we observed some mortality from our low herbicide rate (one third of the labeled maximum rate) among the seedlings. Drift reduction programs for UAVs should consider numerous factors, including nozzle selection and layout, formulation and adjuvants, and the altitude, speed, and direction of flight (P. Chen et al., 2022).

For the potted seedlings, low and high herbicide rates caused statistically indistinguishable levels of injury. This finding underscores the fact that lower herbicide rates are suitable for applications earlier in the season and earlier in weeds' life cycles (Corteva Agriscience, 2023). Diversifying weed management programs, including the incorporation of mechanical and cultural practices, can also reduce total herbicide requirements and the spread of herbicide resistance (Miller, 2016; Neve et al., 2018). Reducing total herbicide requirements will provide both economic benefits to the manager and environmental benefits to the broader ecosystem.

A key limitation of our study was its short timeframe. We tracked only the initial impacts of herbicide applications within a season. Both the efficacy and the non-target impacts of herbicide applications can be short-lived in grassland environments, depending on the initial level of weed invasion, timing of herbicide application, and other management practices (Endress et al., 2012; Lugar et al., 2023; Ortega & Pearson, 2011). Longer-term studies are a key priority for future research. This research may be facilitated by increasingly accurate and cost-effective ways to track rangeland community dynamics using UAVs. Another limitation of this study is the mismatch between in-field plant species and seedling species, since only certain species could be successfully cultivated in the greenhouse. A study where the same species are

used both in the field and as potted seedlings would likely provide meaningful insight into the relationship between life stage and herbicide sensitivity for each species.

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Tables

Table 3. Visual injury scoring system (1 to 10)

Rating		Description	Observable symptoms
1		No visible injury	Plants appear normal; no discoloration, stunting, or deformities.
2		Slight injury	Very subtle leaf curling or slight chlorosis (yellowing); likely not noticeable without close inspection.
3		Mild injury	Light chlorosis on young leaves, slight cupping or twisting, minimal effect on growth. Plant still appears mostly healthy.
4		Moderate injury	Obvious leaf deformation (cupping, puckering), interveinal chlorosis, some stunting, but growth continues.
5		Moderate to significant injury	Deformation and chlorosis more widespread, early leaf drop, slowed growth, some lateral branch dieback.
6		Significant injury	Widespread chlorosis and necrosis, stunted shoots, heavy leaf loss, clear plant stress but not dying yet.
7		Severe injury	Major portions of plant are necrotic or defoliated. Stems may wilt or blacken. Little to no new growth.
8		Near-lethal injury	Most of the plant is dead or dying, with minimal remaining green tissue. May not recover.

9		Extreme injury	Plant is almost completely dead. Only a few live parts remain (e.g., root suckers or basal resprouts).
10		Complete mortality	Total plant death. No green tissue or viable regrowth evident.

Table 4. Number of potted seedlings by combination of species, treatment, and run

Species	High rate	Low rate	Control	Total
Common milkweed	R1: 8	R1: 8	R1: 7	R1: 23
	R2: 11	R2: 9	R2: 11	R2: 31
Sericea lespedeza	R1: 13	R1: 14	R1: 7	R1: 34
	R2: 4	R2: 1	R2: 2	R2: 7
Alyssum	R1: 16	R1: 16	R1: 14	R1: 46
	R2: 20	R2: 13	R2: 19	R2: 52
Common evening primrose	R1: 12	R1: 8	R1: 11	R1: 31
	R2: 4	R2: 9	R2: 0	R2: 13
Baldwin's ironweed	R1: 16	R1: 15	R1: 14	R1: 45
	R2: 20	R2: 12	R2: 17	R2: 49

Table 5. ANOVA results (P values) showing significance of time, treatment, and time-by-treatment effects on percentage cover and visual injury ratings for mature field plants.

	Total forb	Baldwin's ironweed	Goldenrod	Leadplant	Western ragweed	White sagebrush
Percentage cover						

Time	<0.001	0.454	0.784	0.048	0.063	<0.001
Treatment	0.446	0.597	0.417	0.563	0.947	0.116
Interaction	0.040	0.377	0.565	0.118	0.609	0.109
Visual injury score						
Time	NA	<0.001	<0.001	<0.001	0.006	0.545
Treatment	NA	0.476	0.840	0.799	0.915	0.878
Interaction	NA	<0.001	0.011	<0.001	<0.001	0.024

Table 6. ANOVA results (P values) showing significance of time, treatment, and time-by-treatment effects on visual injury ratings for potted seedlings.

	Alyssum	Baldwin's ironweed	Common evening primrose	Common milkweed	Sericea lespedeza
Time	0.001	<0.001	0.002	<0.001	0.001
Treatment	0.104	0.001	0.108	0.007	0.001
Interaction	0.078	0.126	0.238	0.824	0.094

Figures

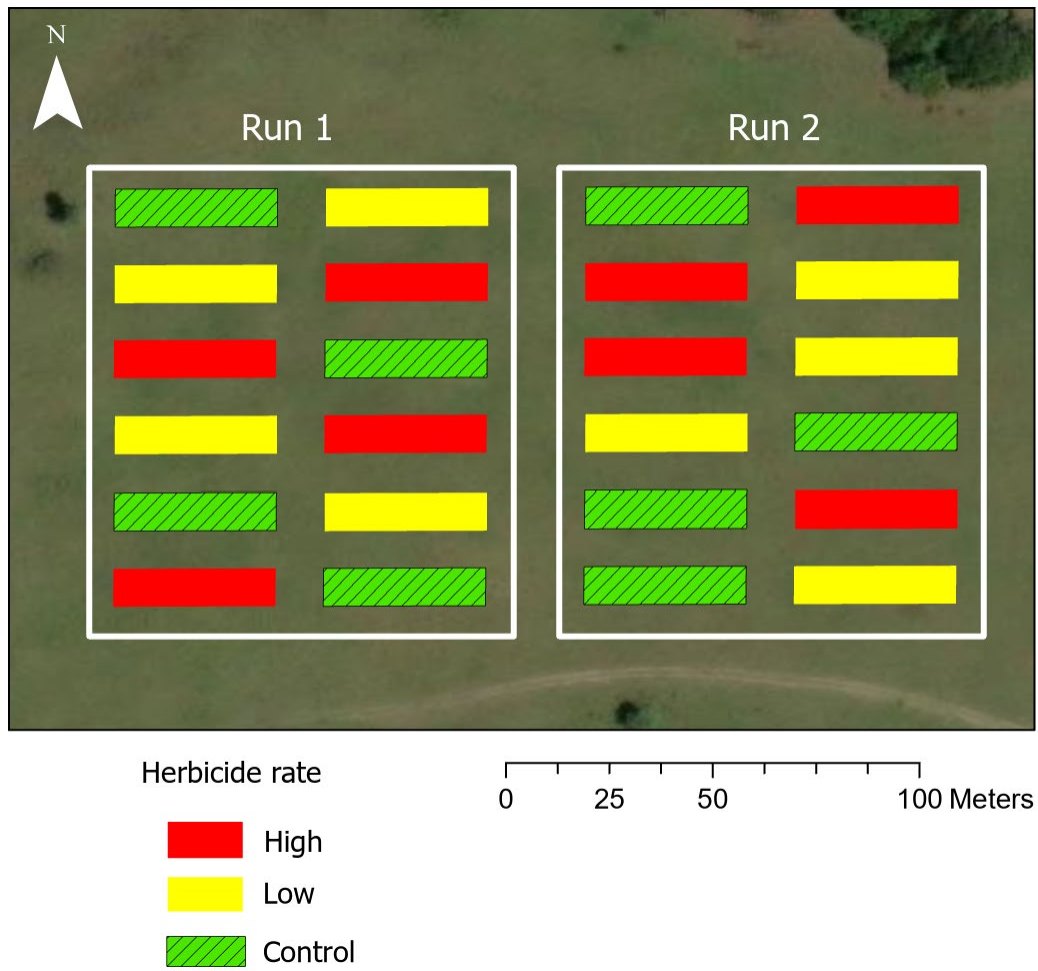


Figure 3.1. Aerial view of the two experimental runs. The colors indicate high (red), low (yellow), and control (green) herbicide rates.



Figure 3.2. A shade cloth structure was constructed using 50% shade cloth atop four 2.4-m steel fence posts.

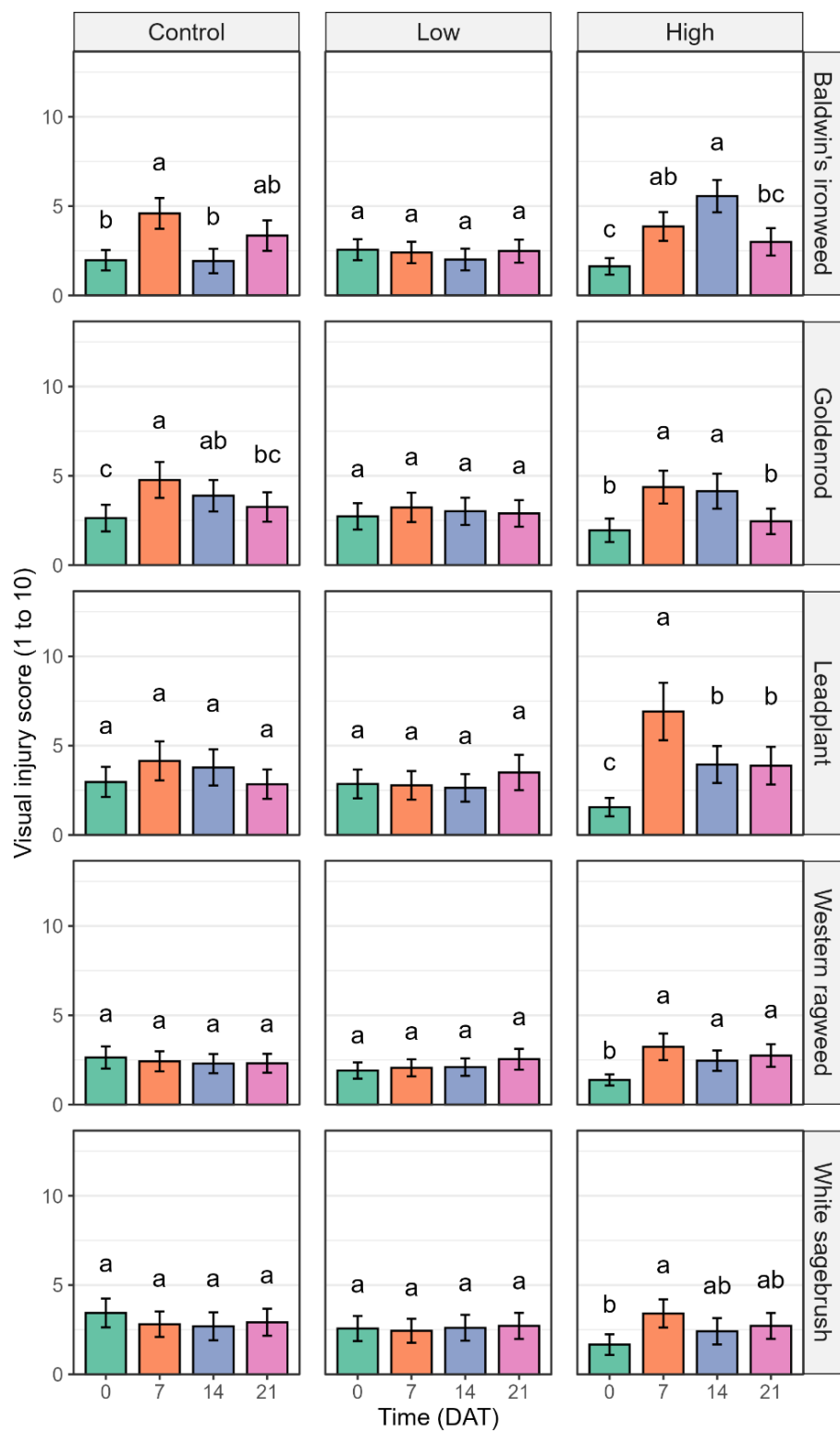


Figure 3.3. Visual injury score (back-transformed estimated marginal means $\pm$ standard error) for mature plants in the field. Within combinations of species and herbicide rate, different letters indicate significant differences between timepoints at $\alpha = 0.05$.

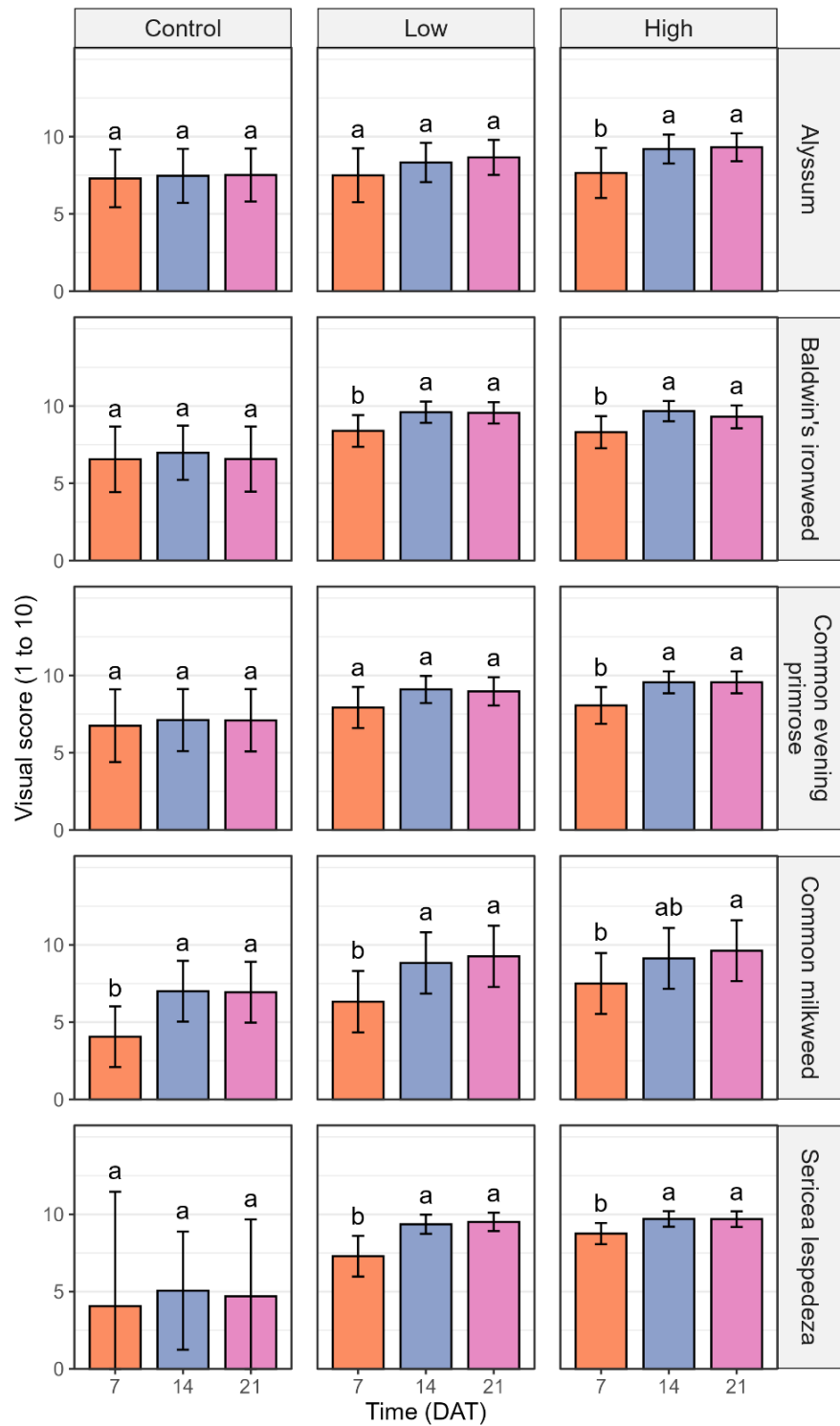


Figure 3.4. Visual injury score (back-transformed estimated marginal means $\pm$ standard error) for potted seedlings. Within combinations of species and herbicide rate, different letters indicate significant differences between timepoints at $\alpha = 0.05$.

Chapter 4

Seedbank Assessment Methods for Sericea Lespedeza [*Lespedeza cuneata* (Dum. Cours.) G. Don]

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Abstract

Sericea lespedeza [*Lespedeza cuneata* (Dum. Cours.) G. Don] is an invasive and noxious legume species originally introduced to the United States for forage and erosion control. This invasive species aggressively outcompetes native species. Its high fecundity and long-lived seeds result in a large, persistent seedbank. Quantifying the *L. cuneata* seedbank in infested areas can help managers select and evaluate weed control measures. There is currently no reliable method of measuring *L. cuneata* abundance in the seedbank. This pilot evaluated several approaches to scarify seeds in the soil, which would break physical dormancy and enable greenhouse emergence assays. Specifically, we tested heat treatments (79°C, 107°C, or 204°C), freeze–thaw cycles (2 or 20 cycles), and mechanical scarification with sandpaper. We hypothesized that 20 freeze–thaw cycles would produce the highest germination rates. Our key finding was that treatment significantly affected germination ($P = 0.006$). High-heat treatments at 107°C and 204°C resulted in no germination, likely due to seed lethality. When these high-heat treatments were excluded, differences among remaining treatments were no longer statistically significant ($P = 0.28$). This pilot study represents a first step towards field quantification of *L. cuneata* seedbanks.

Introduction

Lespedeza cuneata [Sericea lespedeza (*Lespedeza cuneata* (Dum. Cours.) G. Don)] was introduced into parts of the United States beginning in the late 1800s for erosion control and forage (Cummings et al., 2007). It was initially thought to be an appealing forage due to high crude protein content. However, the high tannin content, which makes the crude protein inaccessible, and coarse woody stems make *L. cuneata* unfavorable for livestock grazing (Cummings et al., 2007; Hoveland et al., 1969). *Lespedeza cuneata* is now considered an invasive and noxious weed across many states (Gucker, 2010). It invades rangelands and pastures and reduces forage productivity, forage quality, wildlife habitat, and biodiversity (Brandon et al., 2004; Cummings et al., 2007).

Lespedeza cuneata has many morphological and physiological traits that enhance competitiveness (Ohlenbusch & Bidwell, 2007). It spreads through seed transport via human activity, livestock, and wildlife (Blocksome, 2006; Gucker, 2010). The plant produces up to 30 stems per plant (Pieters, 1939), each of which can potentially produce over 1,000 seeds (Ohlenbusch & Bidwell, 2007). The longevity of *L. cuneata* seeds in the soil seedbank remains largely unknown (Gucker, 2010), with some reports suggesting that *L. cuneata* seeds remain viable in the soil for over 20 (Czarapata, 2005) to 30 years (Fitzgerald et al., 2005). The extended longevity of *L. cuneata* seeds in the soil seedbank poses a major management challenge. For this reason, eliminating an infestation requires repeated control over multiple years (Pile Knapp et al., 2025; Fitzgerald et al., 2005).

Lespedeza cuneata has a low germination rate, often reported at approximately 10–20% for unscarified seeds (Gucker, 2010; Ohlenbusch & Bidwell, 2007; Pieters, 1939). The primary form of dormancy is physical dormancy released by scarification of the seed coat

(Blocksome, 2006; Gucker, 2010). Under natural conditions, scarification is accomplished by freeze–thaw cycles or fire. Although fire often stimulates *L. cuneata* germination, seed mortality occurs at high temperatures (Gucker, 2010; Segelquist, 1971). Under laboratory conditions, manual abrasion or chemical scarification can be used as alternate methods of scarification (Blocksome, 2006; Graham, 1945). A secondary mechanism delaying germination involves germination inhibitors in the seedcoat, which are leached away by soil moisture (Farris, 2006; Logan et al., 1969).

The objective of this study was to investigate how to best encourage scarification and germination of *Lespedeza cuneata* seeds from soil seedbank samples. We hypothesized that heat, freeze–thaw, and mechanical scarification treatments would significantly increase germination of *Lespedeza cuneata* seeds recovered from the artificial soil seedbank compared to untreated controls. Freeze–thaw with 20 cycles was predicted to be the best treatment.

Methods

Artificial Seedbank Preparation

We tested seven treatments: three heat treatments (79°C, 107°C, or 204°C), two freeze–thaw cycles (2 or 20 cycles), mechanical scarification with sandpaper, and control. For each treatment, there were two replicates of 40 seeds.

The soil base for all soil seedbank samples was made using 8.5 parts of field soil and 1.5 parts of sand. The field soil was cropland topsoil collected near Manhattan, Kansas and has a clay loam texture of 22% sand, 51% silt, and 27% clay. The very coarse sand used was initially sifted using a 3mm sieve to remove any large pebbles. The sand and soil were mixed by hand in

a large container and passed through a 9 mm sieve to ensure any large soil aggregates were broken and properly mixed.

Samples were prepared by weighing 250 g of soil base in either small aluminum baking tins or open Ziploc sandwich bags. The soil was allowed to air dry completely at room temperature for 3–4 days. After drying, 40 *L. cuneata* seeds were added to the tray or bag to create an artificial soil seedbank. Any seeds that appeared deformed or disfigured were replaced prior to being added to the soil base. All seeds were derived from approximately 30 *L. cuneata* plants collected from Fort Riley, KS (39.12782, –96.74358) in Fall 2024.

Experimental Treatments

For the heat treatments, a soil seedbank sample was evenly poured and spread within a 33 cm × 23 cm aluminum foil cake pan. The sample was then heated for 15 minutes at 79°C, 107°C, or 204°C. The samples were then removed from the oven and allowed to cool to room temperature before being repacked for planting.

For the freeze–thaw treatments, 10 mL of tap water was added to a Ziploc bag containing the soil seedbank sample. The bag was then gently massaged for 30 seconds to incorporate all the water, rehydrating the soil. Excess air was removed from the bag, and the bag was sealed. For each freeze–thaw cycle, the sample was placed in the freezer at –18°C for 2 hours, then removed and placed on the counter at room temperature for an additional 2 hours to completely thaw. Two freeze–thaw treatments were implemented: 2 cycles versus 20 cycles. After the sample was brought back to room temperature following the last cycle, it was ready for planting.

For mechanical scarification, a soil seedbank sample was poured and spread thinly within an aluminum baking tray. Using 120-grit sandpaper, the soil–seed mixture was abraded by placing the sandpaper facedown and rubbing in small circles around the tray while maintaining even pressure and contact with the soil using a flat hand. The pan was occasionally shaken gently to redistribute the soil and seeds evenly across the tray before continuing abrasion. After 2 minutes, the abrasion ceased, and the sample was ready for planting.

Data Collection

Prior to adding the sample, 28 cm × 58 cm trays were filled with ~3 cm of potting mix (Berger, Saint-Modeste, Quebec) and 2.5 mL of slow-release 12-4-8 N-P-K (Miracle-Gro Shake ‘n Feed all-purpose fertilizer; Scotts Miracle-Gro, Marysville, Ohio). Each soil seedbank sample was thinly spread across the entire tray, then gently disturbed with fingertips to work it into the top 0.64 cm of potting soil. The samples were kept in a climate-controlled greenhouse at 24°C during the day and 18°C at night under natural light (Figure 4.1A). The samples were watered daily for four weeks. Throughout this time, the emergence of *L. cuneata* seedlings was recorded weekly. Once positively identified, the seedlings were counted and removed (Figure 4.1B).

Statistical Analysis

Statistical analysis was performed in R version 4.4.2 (R Core Team, 2024). Generalized linear mixed models (package “lme4”) with a Poisson family and log link were used to evaluate the impact of scarification treatment on total germination. Diagnostics

were assessed with simulated residuals (package “DHARMA”), significance was assessed with ANOVA at $\alpha = 0.05$, and post-hoc comparisons were carried out using Tukey’s HSD (package “emmeans”).

Results and Discussion

Treatment of the soil seedbank significantly affected seed germination of *Lespedeza cuneata* ($P = 0.006$; Figure 4.2). However, post-hoc comparisons were not significant according to Tukey’s HSD. When the two high-temperature treatments that resulted in no seed germination (107°C and 204°C) were excluded from the analysis, treatment effects were no longer significant ($P = 0.28$).

The greatest germination occurred in the freeze–thaw treatment with 20 cycles, with 8 of 80 seeds germinating across the two replicates (Figure 4.2; Table 1). By contrast, the freeze–thaw treatment with 2 cycles resulted in 3 of 80 seeds germinating. Mechanical scarification and the 79°C heat treatment also resulted in 3 of 80 seeds germinating. The control treatment resulted in 2 of 80 seeds germinating and no seeds germinated in the 107°C or 204°C heat treatments.

Overall, germination rates were low across the entire experiment. The highest observed germination rate was 10% of seeds germinating after 20 freeze–thaw cycles. This rate of germination aligns with the 10–20% germination rates for unscarified seeds reported in prior studies (Gucker, 2010; Ohlenbusch & Bidwell, 2007; Pieters, 1939). It is possible that the seed lot was less than 100% viable, so that the highest rate of germination from our study matched the lowest rate of germination from other studies. The finding that freeze–thaw produced the (numerically) highest germination was consistent with the known potential of freeze–thaw cycles

to stimulate *L. cuneata* germination (Davidson & Kilgore, 2005). Likewise, Young (2000) found that three freeze–thaw cycles significantly increased *L. cuneata* germination.

The heat treatments led to low germination, with low germination at 79°C and no germination at 107°C or 204°C. The lack of germination in the higher-heat treatments could be attributed to seed mortality. Bell (2012) found that an oven temperature of 250°C for 2 minutes was lethal to *L. cuneata* seeds. Mortality occurred after 1 minute at 325°C, 30 seconds at 375°C, and 15 seconds at 450°C (Bell 2012). A similar study by Martin et al. (1975) found that 4 min of exposure to moist or dry heat at 90–110°C appeared to be lethal to sericea lespedeza seeds. Taken together, these results suggest that prolonged exposure to temperatures above approximately 80–90°C is likely to kill *L. cuneata* seeds. Although prescribed fires exceed these temperatures at the soil surface, soil acts as a protective insulator for seeds within the seedbank over just a few centimeters.

Although some germination was observed from the mechanical scarification treatment, there was no clear difference from the control. One major obstacle with this approach is the physical obstruction that soil poses during the abrading process, limiting contact between the sandpaper and seeds. Abrasion by soil particles alone is not thought to be an effective form of scarification (Baskin & Baskin, 2000). A longer period of abrasion or a thinner layer of soil might have enhanced germination from this treatment.

Although this pilot study indicated an effect of scarification treatment on seed germination of *L. cuneata* in soil, these results are based on a small number of replicates per treatment. A better understanding of how to induce germination of *L. cuneata* from gathered soil samples can facilitate future seedbank assessments, leading to better monitoring and eradication of *L. cuneata* infestations.

Acknowledgements

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Tables

Table 7. Recorded germination of *Lespedeza cuneata* seeds from the soil seedbank under various scarification treatments over a four-week period.

Treatment / Replicate	Week 1 (10/28/26)	Week 2 (11/4/26)	Week 3 (11/11/26)	Week 4 (11/18/26)	Total
Control / A	0	1	0	0	1
Control / B	0	0	1	0	1
Heat 175°F / A	0	1	0	0	1
Heat 175°F / B	0	0	2	0	2
Heat 225°F / A	0	0	0	0	0
Heat 225°F / B	0	0	0	0	0
Heat 400°F / A	0	0	0	0	0
Heat 400°F / B	0	0	0	0	0
Freeze–Thaw (20 cycles) / A	0	1	4	0	5
Freeze–Thaw (20 cycles) / B	0	0	3	0	3
Freeze–Thaw (2 cycles) / A	0	0	0	0	0
Freeze–Thaw (2 cycles) / B	0	1	2	0	3
Mechanical / A	1	0	0	0	1
Mechanical / B	0	2	0	0	2

Figures

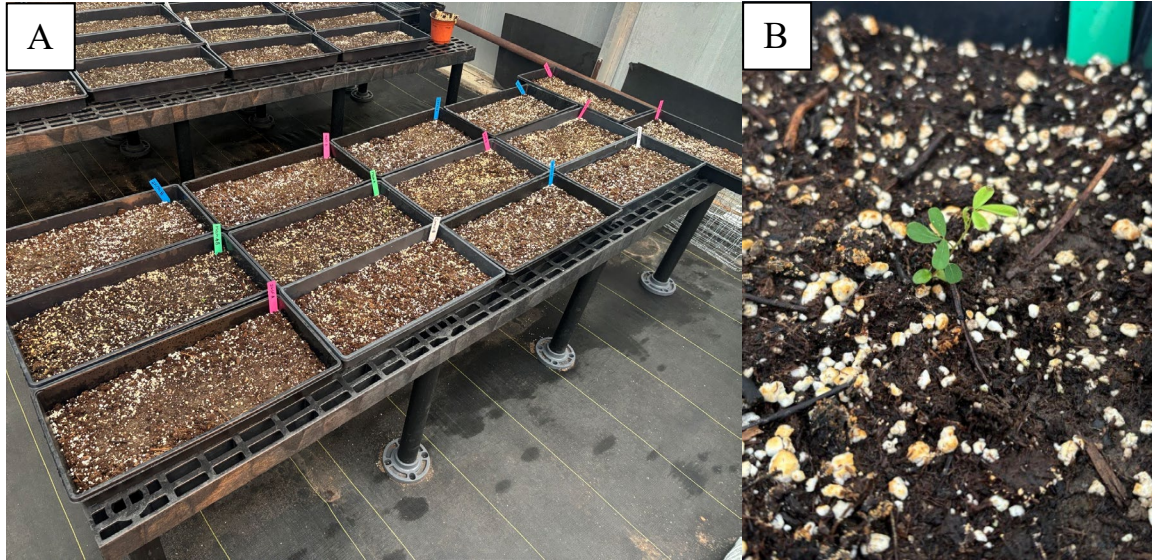


Figure 4.1. (A) Trays of planted *Lespedeza cuneata* seedbank samples in the greenhouse. (B) Emerged *L. cuneata* seedling.

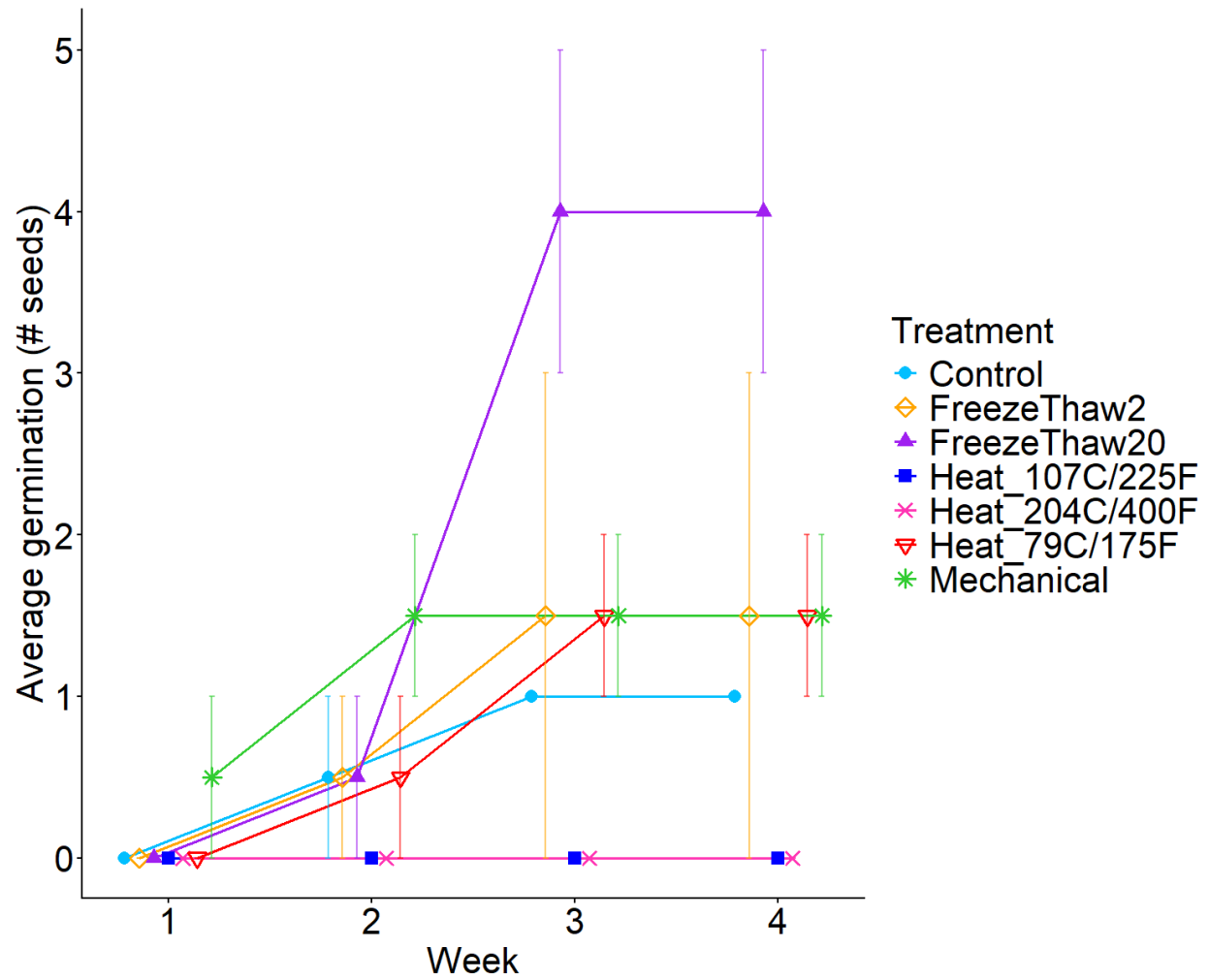


Figure 4.2. Average germination of *Lespedeza cuneata* seeds by scarification treatment