TREE CANOPY AND LIVESTOCK GRAZING INFLUENCES GRAMINOIDS IN THE

SOIL SEED BANK

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ABSTRACT

Understanding seeds and how they respond to the environment and land-use is a crucial part of plant population dynamics. The objective of my study is to determine the effects of livestock grazing and canopy densities on graminoid soil seed bank densities in a ponderosa pine-bunchgrass ecosystem in northern Arizona. Using a long-term, active livestock exclosure, I stratified the site into four combinations of livestock grazing activity (grazed, ungrazed) and tree canopy cover (open park, under tree canopy) to understand how these factors may contribute to the soil seed bank's presence and abundance. Using the seedling emergence method, I collected and processed soil samples from these four groups. I found nine graminoid species in total in the seed bank; one annual and eight perennials – one from *Cyperaceae* and eight from *Poaceae*. Seed bank emergence varied between grazed and ungrazed plots, however, tree canopy cover had no significant effect. Ungrazed plots averaged 1.25 and 1.0 emergent graminoid seedlings per transect for Park and Tree canopy cover designations, respectively. Grazed plots averaged 16 and 23 emergent graminoid seedlings per transect for Park and Tree canopy cover types, respectively. My study adds to the larger body of seed bank literature currently being developed to provide insights to policymakers and managers involved in livestock grazing and grassland conservation.

Key Words: *Pinus ponderosa*, bunchgrass, long-term grazing exclosure, Arizona, Fry Park

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INTRODUCTION

Seeds are crucial to the persistence of populations and are a driving factor in determining the biological and genetic diversity of plant communities (Ooi 2012). Seed production, fecundity and seed storage are all key factors in the persistence of plant populations, and while we understand the importance of seeds, many aspects of how seeds function and affect plant populations are still unknown (Begon et al. 2009). Seed ecology research is focused on seed-related life cycles and how those cycles may affect the persistence of plant populations, especially with changing climate and land use.

One of the key components of seed ecology is viability, composition, and density of seeds in the soil seed bank. Previous studies in ponderosa pine – bunchgrass systems of northern Arizona have studied the composition and viability of the soil seed bank and uncovered a high number of annual forbs (Korb et al. 2005; Abella et al. 2007; Abella and Springer 2008; Abella 2022). In addition to composition and viability of the soil seed bank, early work showed that there is low synchronicity between aboveground vegetation and the soil seed bank, with only three monocot species out of 19 total emergent species (Korb et al. 2005). However, a more recent study showed that there is more synchronicity than initially thought, and the unique climate of the ponderosa pine forest type may allow more perennial species to succeed in the soil seed bank (Abella 2022). In a more comprehensive analysis of the region, researchers found 49 total species in the soil seed bank, with 10% exotic, and 43% native perennials (Abella and Springer 2008). This study additionally found 583 seeds per square meter in plots with a closed tree canopy, and 1611 seeds per square meter in plots with open tree canopies (Abella and Springer 2008).

The idea that livestock grazing may have an effect on soil seed banks is not new, but studies have mixed results (Kinucan and Smeins 1992; Sternberg et al. 2003; Aboling et al. 2008). One of these studies suggested that perennial graminoids use the soil seed bank in ungrazed areas while areas with heavy grazing activity primarily have ruderal dicots in their seed banks (Kinucan and Smeins 1992). Another study pointed towards graminoids tolerance of moderate grazing, but still having higher densities of seeds in the seed bank in ungrazed areas (Sternberg et al. 2003). Finally, the most recent of these studies noted that annual and perennial graminods were the most present in the seed bank when grazed later in the growing season, while short annual grasses and forbs avoided livestock grazing early in the growing season (Aboling et al. 2008). This objective of my study is to determine the effects of livestock grazing on the soil seed bank under varying ponderosa pine tree canopies inside and outside a long-term grazing exclosure in Fry Park in northern Arizona.

METHODS

Study Area

My soil seed bank data were collected within and adjacent to an active livestock exclosure located on the edge of Fry Park. Fry Park is located in northern Arizona (latitude 35°4′N, longitude 111°47′W) on the Coconino National Forest approximately 19 km southwest of Flagstaff, Arizona and is at 2170 m elevation. Precipitation is bimodal with averages of 56 cm as rain and 259 cm of snow; however, currently this area is experiencing prolonged drought (Staudenmaier et al. 2014; Arizona Department of Water Resources 2022). The parent material at Fry Park is basalt and cinders, and the soil is a Typic Argiboroll with a loam soil texture (Miller et al. 1995). The overstory trees are pure ponderosa pine (*Pinus ponderosa*), although

Gambel oak (*Quercus gambelii*) are scattered throughout the area. The understory is dominated by perennial bunchgrasses, such as black dropseed (*Sporobolus interruptus),* mutton bluegrass *(Poa fendleriana),* and mountain muhly *(Muhlenbergia montana)* (Bakker et al. 2010).

The active livestock exclosure is located on the northwest portion of Fry Park and is 0.8 ha in size (55 m by 143 m). This exclosure lies along the boundary between park (upland montane grassland) and tree (forest) habitats (Figure 1). This exclosure is part of the network of Hill Plots livestock exclosures, which were originally established in 1912 (Arnold 1950; Bakker et al. 2008; Bakker et al. 2010). It was built and maintained to exclude cattle, but it does not exclude wild ungulates such as elk and deer. Currently, cattle graze the Fry Park study area for three weeks each summer. In 2020, 485 cows, calves and bulls were present from 01 August to 20 August (Peck 2020).

Fry Park and the surrounding area were logged in 1910 (Arnold 1950). When the exclosure was established in 1912, tree density did not differ, however by 2002-2004, tree density was greater inside the exclosure due in part to survival of ponderosa pine regeneration (Bakker and Moore 2007).

I have preliminary data on the graminoid (grasses and grass-like plants) soil seed bank in ponderosa pine-bunchgrass ecosystems from six study sites in northern Arizona (Traver and Moore 2021). It was apparent in this preliminary study that one site, Fry Park, was "performing better" than the other sites, with nearly ten times the emergent graminoid seedlings as the other sites. Fry Park is unique because it has an active, long-term, livestock grazing exclosure, so I decided to test whether the graminoid seed bank was different within and outside the exclosure.

Field Methods

Soil seed bank samples were collected within and adjacent to the Fry Park livestock exclosure from June 3 to June 4 of 2021. My study followed the original study design of Bakker et al. (2010), which included sampling within four treatments: park grazed (PG), park ungrazed (PU), tree grazed (TG) and tree ungrazed (TU). For my seed bank study, I selected two 8 x 12 m treatment plots in each treatment combination, which were plots 1 (PG1, PU1, TG1 and TU1) and plots 3 (PG3, PG3, TG3 and TU3) (Figure 1). I selected plots that were farthest apart from each other to ensure the entire study area was well represented.

Two 12-meter line transects were established within each treatment plot. I collected soil sample cores along these two transects using a modified point-intercept method. That is, any time one of the transects intersected with a target perennial graminoid species, two soil cores were taken, an "interspace" sample and a "parent plant" sample. Soil cores were taken with a 4.2 cm diameter lead pipe and sledgehammer at a depth of 10 centimeters (Abella et al. 2007). The nine target species are common perennial bunchgrass species and include: blue grama (*Bouteloua gracilis),* white mountain sedge *(Carex geophila),* bottlebrush squirreltail *(Elymus elymoides),* Arizona fescue *(Festuca arizonica),* prairie junegrass *(Koeleria macrantha),* mountain muhly *(Muhlenbergia montana),* pine dropseed *(Muhlenbergia tricholepis),* mutton bluegrass *(Poa fendleriana),* and black dropseed *(Sporobolus interruptus).*

When an individual of the target species was encountered along the line transect, two soil cores were taken, where one core was taken from directly on top of the plant ("parent plant" sample), and the second core was taken in the nearby interspace, 0.5 m away within bare mineral soil. Soil cores from each sample type were composited and stored in a refrigerator at 34 degrees Fahrenheit for 5 weeks to account for any possible seed cold stratification needs.

Emergence values were converted to seeds per m^2 by multiplying the number of cores taken in each sample by the surface area one 4.2 cm diameter core covers. Tree canopy cover data were collected using a densitometer in each plot (Adikari and MacDicken 2015). Plant nomenclature follows the SEINet Arizona-New Mexico chapter (SEINet Portal Network 2021).

Greenhouse Methods

Soil seed bank samples from field collections were quantified using the seedling emergence method (Brown 1992). I used the seedling emergence method because seedling emergence is more representative of seedlings that would emerge on-site than seed extraction, and the emergence method has been used in previous soil seed bank research of the region (Korb et al. 2005; Abella et al. 2007). Soil samples were spread within "ten-twenty" greenhouse trays, with a volume of 9688 cm^3. Standard potting soil mix (NAU Research Greenhouse Complex) was used, which is a 1:2:1 ratio of peat moss, perlite and vermiculite, respectively. Trays were filled with 3-4 inches of potting mix, with a 1-2 cm layer of soil seed bank samples spread over the top.

Samples were watered daily from 04 October to 08 November 2021, and emergent graminoid seedlings were marked and identified as soon as possible. I decided to conduct this "grow-out" for five weeks based on information available for the germination timing of known seed lots of the target graminoid species (Western Native Seed 2021).

Statistical Analysis

I used a two-way Analysis of Variance (ANOVA) to determine the significance of tree canopy and grazing effects on the soil seed bank. My data did not follow the traditional

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assumptions of normality for statistical inference in ANOVA due to a high number of zero counts. To account for this, I used permutation methods of statistical inference in place of the usual ANOVA F-tests. P-values for tests of significance are determined by bootstrapping using the lmPerm R package, which was designed to obtain P values for linear models and ANOVAs from permutations (Wheeler and Torchiano 2016).

RESULTS

Species Composition of Graminoid Soil Seed Bank

Nine graminoid species were detected in the soil seed bank samples. Eight species are from *Poaceae,* and one species is from *Cyperaceae*. Eight species are perennials, and one species is an annual. All species are native graminoids. Over 50% of emerged species were C4 graminoids. *Muhlenbergia minutissima*, a native, annual, C4 graminoid, had the highest number of seeds in the soil seed bank, with 52 emergent seedlings (Table 1). I did not find any invasive graminoid species in the soil seed bank.

Distance from the Parent Plant's Effect on Presence in the Soil Seed Bank

Generally, emergence rates were higher when sourced from "Parent Plant" samples than when sourced from "Interspace" samples (Table 2). The largest exception to this trend is *Bouteloua gracilis*, which has equal amounts of emergent seedlings from the two sample types (Interspace vs. Parent Plant).

Tree Canopy Cover Values' Effect on Soil Seed Bank

When emergence results were stratified by tree canopy cover type (tree vs. park), it was evident that most seedlings of C4 graminoid species emerged from the grass-dominated park (Figure 2), while most C3 graminoids' successful seedlings were found overwhelmingly in tree plots. No significant difference was found between the number of seedlings emerged from the seed banks of tree plots and park plots when species composition is ignored (Figure 3).

Park plots had 0% tree canopy cover. Ungrazed tree plots (TU1 and TU2) had a tree cover of 77%. In grazed tree plots (TG1 and TG2) cover ranged from 35% to 47%, respectively.

Livestock Grazing's Effect on Graminoid Soil Seed Bank

Livestock grazing activity had a strong effect on graminoid seeds' presence in the seed bank (Figure 3), with soil samples from grazed areas yielding an average of 765.5 seeds per square meter, while ungrazed transects yielded a maximum of 44 seeds per square meter (Table 3). Livestock grazing activity had an effect on species richness of the soil seed bank (Table 3).

Interaction between Tree Canopy and Livestock Grazing

Livestock grazing activity had a greater significant effect on the soil seed bank; although the interaction of tree canopy cover showed an increase of seedling count from grazed park plots to grazed tree plots, and a decrease of seedling count from ungrazed park plots to ungrazed tree plots (Figure 4). Through use of two-way ANOVA, livestock grazing activity's effect on the soil seed bank yielded a P-value of 0.013, while tree canopy cover's effect yielded a P-value of 0.242. The interaction between these two variables yielded a P-value of 0.292.

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DISCUSSION

Species Composition of Graminoid Soil Seed Bank

This study focused on the graminoid component of the soil seed bank at Fry Park. The seed bank was dominated by nine native graminoid species that also occurred in the aboveground herbaceous vegetation at this site (Bakker and Moore 2007, Bakker et al. 2010). *Muhlenbergia minutissima*, a native, C4, annual graminoid had the highest count of seedlings in the soil seed bank. *Bouteloua gracilis*, *Elymus elymoides*, *Koeleria macrantha* and *Poa fendleriana* had similar emergence to each other, with *B. gracilis* emerging almost exclusively from grazed park plots, while *E. elymoides* and *P. fendleriana* had a strong relationship with grazed tree plots. *K. macrantha*'s emergence was spread evenly over both grazed plots and ungrazed tree plots (Figure 2). Other graminoid species that emerged with lower values include *Festuca arizonica, Carex geophila*, *Muhlenbergia montana,* and *Sporobolus interruptus*. These species mostly emerged from grazed tree plots, with *S. interruptus* emerging evenly from grazed park and tree plots, but in low quantities.

It is not surprising that *M. minutissima* had the greatest number of emerged seedlings of the graminoids in the soil seed bank since it is an annual, ruderal species that is adapted to disturbance, and relies on soil seed bank for survival (Abella and Springer 2012). Fry Park has soil with a high clay content, leading to shrink-swell dynamics that depend on the fluctuation of soil moisture (Bakker et al 2010). Fry Park's soils are additionally disturbed by livestock grazing activity in areas outside the grazing exclosure (Bakker et al 2010). Such high levels of disturbance in the soils in Fry Park likely led to success for this annual species.

It should be noted that *Muhlenbergia tricholepis* is easily misidentified as *M. minutissima* and has not appeared in the soil seed banks of other regional studies (Korb et al. 2005; Abella

and Springer 2008, Abella and Springer 2012). Given the previous lack of *M. tricholepis,* any suspected *M. tricholepis* seeds were marked as *M.* minutissima. The majority of seedlings observed in this study were likely *Muhlenbergia minutissima* seedlings, however, it is possible that *Muhlenbergia tricholepis* seedlings were included due to misidentification.

Recent studies on soil seed banks in ponderosa pine forests noted that this forest type has high levels of synchronicity with the contemporary aboveground vegetation, more so than that of other western ecosystems (Abella 2022). It is suggested that the semi-arid climate of this forest type allows for preservation of perennial seed banks, triggering annual seed bank populations, while making soil seed bank storage practical for perennial species that are drought sensitive. I may be seeing evidence of this in my results, as there are notably high numbers of perennial graminoid species in the soil seed bank that, when given the opportunity, emerged from their dormant state.

Distance from the Parent Plant's Effect on Presence in the Soil Seed Bank

Generally, in this study, emergent seedlings had a higher presence in parent plant samples. This was expected, as they are directly adjacent to a seed source. Since parent plant samples were composited across one transect, I cannot attribute specific plants' "parent" emergence with mature plants of that same species. Despite this, I can make some inferences regarding wind dispersal of graminoid seeds. Typically, seeds in the soil seed bank are small and rounded, which are not the same seed traits used for wind dispersed seeds (Baskin and Baskin 2014). A dynamic of wind dispersal is – like rocks, trees or any other form of shelter – larger bunchgrasses may act as windbreaks and "catch" seeds blowing in the wind. Seed dispersal

behavior like this would explain the high emergence rate of species known to have wind dispersed seeds, such as *B. gracilis*, or *E. elymoides*.

A species found at similar frequencies between parent plant and interspace samples was *Bouteloua* gracilis. This change in pattern from other emergent species is likely due to *B. gracilis*'s hairy seed (Figure A.1), allowing for better short-range wind dispersal than a smooth, heavy seed, such as that of *Carex geophila*. *C geophila*'s flowers are typically buried within the parent plant, at heights of a couple centimeters, further reducing their wind dispersal capability (Partridge 2021).

Tree Canopy Cover Values' Effect on Soil Seed Bank

The perennial graminoid with the highest count of emergent seedlings was *Elymus elymoides*, followed by *Bouteloua gracilis*. These species are also the highest emergent perennial species in the C3 or C4 photosynthetic pathways, respectively. C4 graminoids are generally more drought tolerant than C3 graminoids (Monson et al. 1986). Based on this information, it would make sense for C4 graminoids to be able to survive, flower and reproduce in the open, hotter, drier park conditions, while C3 graminoids would stay more competitive within the shelter of areas with significant tree cover.

While specific graminoids may be favored in shaded areas over others, herbaceous cover decreases with increasing tree canopy cover, with herbaceous cover under 10% tree canopy cover being roughly 5.5 times the herbaceous cover under 100% tree canopy cover (Arnold 1950). A recent study of the Fry Park study site show that park plots contain 27-29% herbaceous basal cover, while tree plots only contain 1-4% herbaceous basal cover (Bakker et al 2010). Forb cover did not differ between plots, with graminoid cover making up the bulk of the difference. In

contrast, I had a differing result to Bakker et al. (2010) in that graminoid seedling emergence in my study did not differ between tree vs. park plots but did differ between plots that were disturbed (grazed vs ungrazed). In ungrazed plots, more seeds emerge in open plots than closed plots, similar to the results of Abella and Springer's work in 2008. The reverse is true in grazed areas though, with seed densities in Tree Grazed plots doubling those of Park Grazed plots (Abella and Springer 2008).

Livestock Grazing's Effect on Graminoid Soil Seed Bank

Graminoid emergence shows livestock grazing treatment as a significant factor in the presence of the seeds in the soil seed bank at Fry Park. Historical studies discuss the effects of livestock grazing on bunchgrasses at multiple sites throughout northern Arizona's ponderosa pine forests, including Fry Park (Arnold 1950; Bakker et al 2010). Through the separation of Fry Park into four combinations of two treatments, I was able to identify livestock grazing as a significant contributor to seed bank presence. Grazed plots had a higher amount of viable and active graminoid seeds in their soil seed banks. Possible effects of livestock grazing may be linked to heightened seed bank presence. These might include soil compaction, removal of competition, or effects on individual plants that promote seed production. However, quantifying these factors was beyond the scope of my study.

Early observations in the region indicate that certain perennial bunchgrass species can escape and withstand grazing better than others, namely *Bouteloua gracilis*, *Elymus elymoides* and *Sporobolus interruptus* (Arnold 1950; Briske 1996). While *S. interruptus* had extremely limited emergence in my trials, *B. gracilis* and *E. elymoides* were the two most common perennial species in my results – emerging exclusively from grazed plots. It is possible that these

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species' success in grazed areas mean that they can allocate more resources to reproduction while other species that cannot tolerate grazing, such as *Muhlenbergia montana* and *Festuca arizonica* have a lower count of emergent seedlings.

Livestock grazing also increased species richness of the soil seed bank in my study, with grazing activity at least doubling number of graminoid species (Table 3). While other seed bank studies in the region often compare aboveground vegetation and belowground composition, my study lacks sufficient data to do so.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Graminoid seedling emergence for all nine species was greater or exclusively present in grazed areas at Fry Park. While we may speculate as to why certain species' seed bank performance in grazed areas was greater, other impacts of livestock grazing must be considered, as well as other biotic and abiotic factors such as drought. Unfortunately, my study does not contain sufficient data to make further claims on the intricacies of livestock grazing's effect on graminoid seed banks.

Future studies on the soil seed bank in the ponderosa pine-bunchgrass rangelands should consider the role of livestock grazing. Future studies might include small experimental pastures with different grazing intensities, where livestock numbers and season of use can be controlled. In addition to examining grazing intensity and season of use, other soil-related variables, which also affect seeds in the seed bank should be measured, such as soil bulk density, soil moisture, soil temperature, aggregate stability or soil texture because these variables might affect soil seed bank presence more than grazing, per se (Haight et al. 2019). It is possible that livestock grazing-related activities may be beneficial for creating and retaining strong soil seed banks of native

annual and perennial graminoids. Previous studies have reported livestock grazing as harmful to graminoid species, especially their flowering capability (Kerns et al. 2011; Davidson et al. 2020). Contrary to this evidence, some studies show that livestock grazing activity does not influence flowering capability of graminoids, and removal of grazing after prolonged periods can increase the number of flowers produced in following years (Spence et al. 2014; Elwell et al. 2016). Timing and intensity of grazing may have an impact too, with Sternberg et al. (2003) noting that livestock grazing reduced soil seed bank density the most when grazing was conducted during the seed set period. Another study in the Mediterranean shows that perennial grass seed banks had a higher number of emergent seedlings when grazed later in the season (Aboling et al. 2008). In a global meta-analysis of livestock grazing's effects on soil seed bank, it was found that light grazing activity could benefit soil seed banks, with moderate grazing having no effect – high-intensity grazing though, did negatively impact soil seed banks (Shi et al. 2022).

Stronger seed banks could act as a "safety net" for disturbances, allowing for resurgence of these species after non-fire disturbances, such as drought (Abella 2022). This could reduce costs by lowering the need for planting of species, while simultaneously reducing the risk of introducing invasive species like *Bromus tectorum* or *Hordeum jubatum*.

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TABLES

Table 1. Counts of graminoid species with emergent seedlings in greenhouse trials.

Species	Seeds per m^2	Photosynthetic Pathway
Muhlenbergia minutissima [1]	123.50	**C4**
Elymus elymoides	54.63	**C3**
Bouteloua gracilis	52.25	**C4**
Koeleria macrantha	45.13	**C3**
Poa fendleriana	45.13	**C3**
Festuca arizonica	30.88	**C3**
Carex geophila	21.38	**C3**
Muhlenbergia montana	11.88	**C4**
Sporobolus interruptus	4.75	**C4**
Total	**389.53**	

[1] The majority of seedlings were *Muhlenbergia minutissima* seedlings, however, it is possible that *Muhlenbergia tricholepis* seedlings were included.

Table 2. Emergence of graminoid seedlings by species, sorted by sample type (interspace vs. parent plant).

Species	Interspace seeds per m^2	Parent plant seeds per m^2
Muhlenbergia minutissima	90.25	156.75
Elymus elymoides	14.25	95
Bouteloua gracilis	52.25	52.25
Koeleria macrantha	19	71.25
Poa fendleriana	19	71.25
Festuca arizonica	19	42.75
Carex geophila	4.75	38
Muhlenbergia montana	4.75	19
Sporobolus interruptus	4.75	4.75
Total	**228**	**551**

Table 3. Seed density and species richness, stratified by plot type

Plot Type	Seeds per m^2	α richness
Park Grazed	460.11	5
Park Ungrazed	44.03	2
Tree Grazed	1,071.39	9
Tree Ungrazed	24.89	1
Total	389.53	9
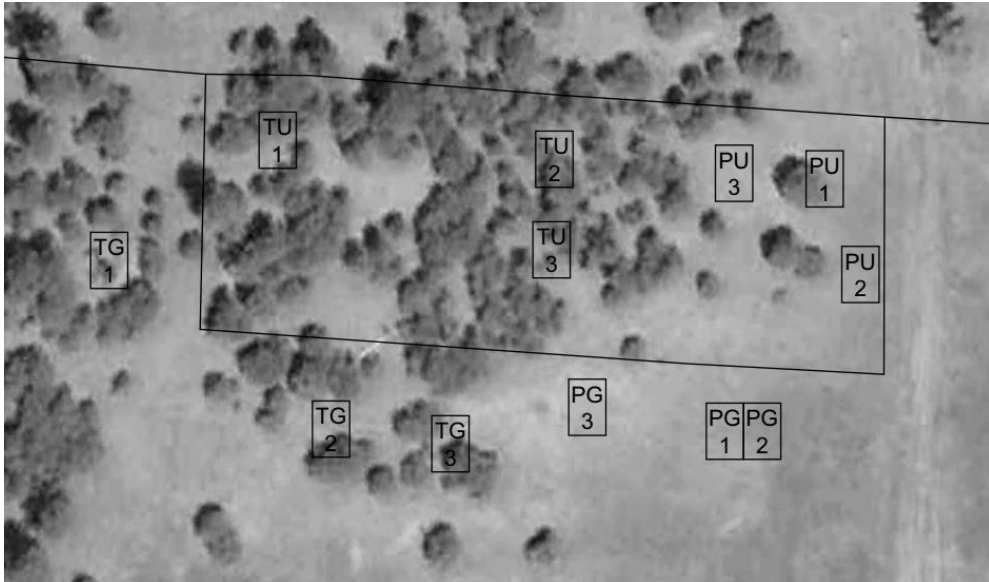
Figure 1. Location of Fry Park's exclosure and plot locations from Bakker et al. (2010). Plots were located within four treatments including park grazed (PG), park ungrazed (PU), tree grazed (TG) and tree ungrazed (TU). For this soil seed bank study, plots 1 (PG1, PU1, TG1 and TU1) and plots 3 (PG3, PG3, TG3 and TU3) were sampled. Aerial photograph and drawings from 2005.
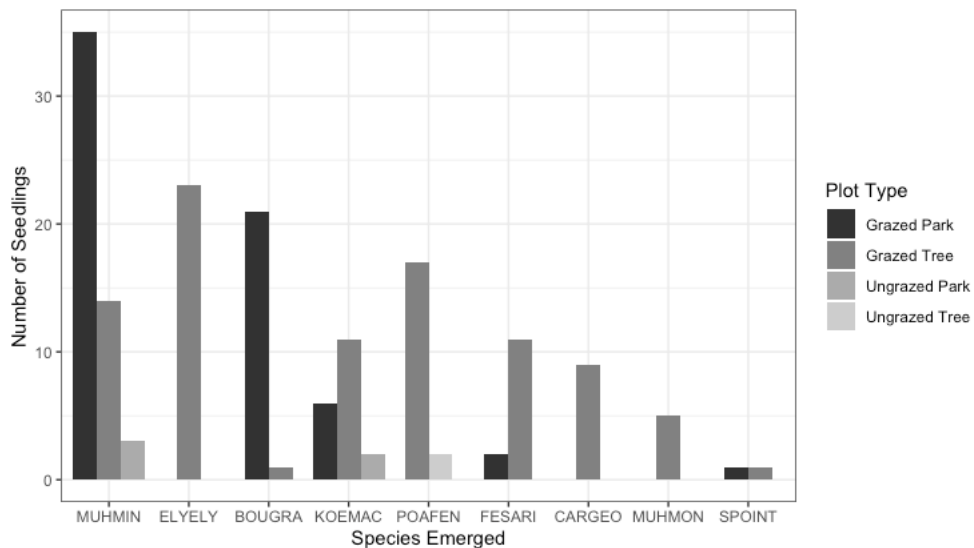
Figure 2. Total emergence of graminoid seedlings by species, sorted by treatment plot type (park vs. tree, grazed vs. ungrazed).
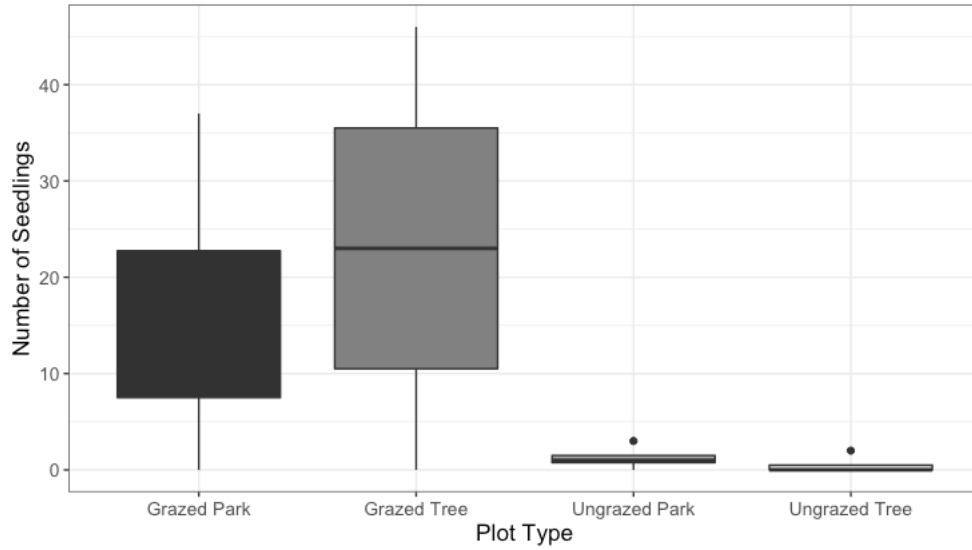
Figure 3. Total seedling emergence counts, sorted by treatment plot type (park vs. tree, grazed vs. ungrazed). One point represents the count of seedlings emerged from one transect.
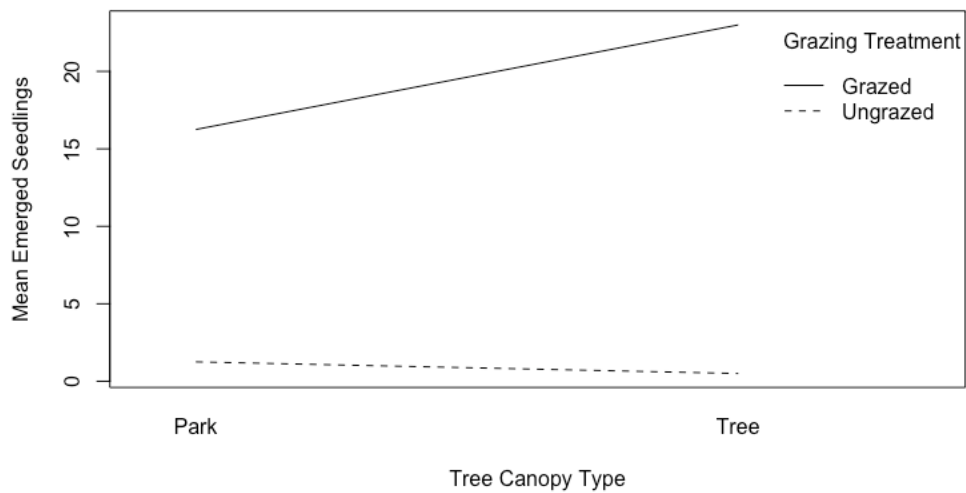
Figure 4. Interaction between the effects of tree canopy cover and livestock treatment (grazed vs. ungrazed) on seed bank emergence. Two-way ANOVA, with livestock treatment P-value = 0.013, while tree canopy cover P-value = 0.242, and the interaction p-value = 0.292.
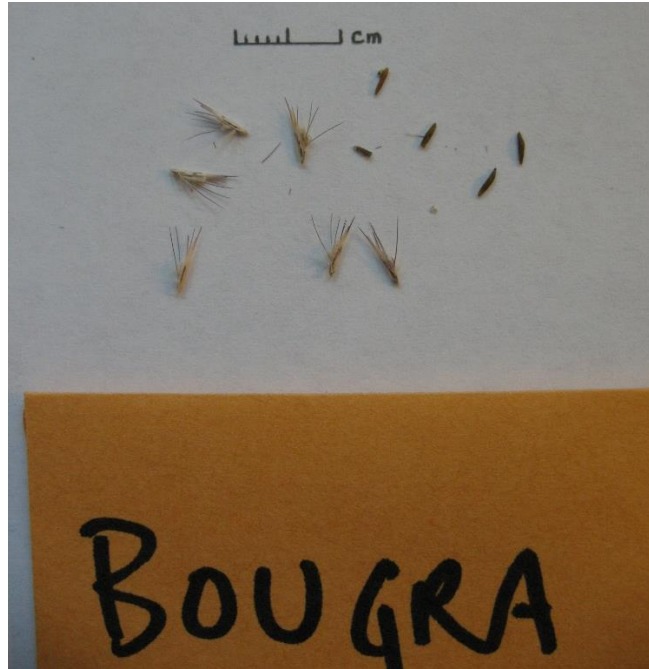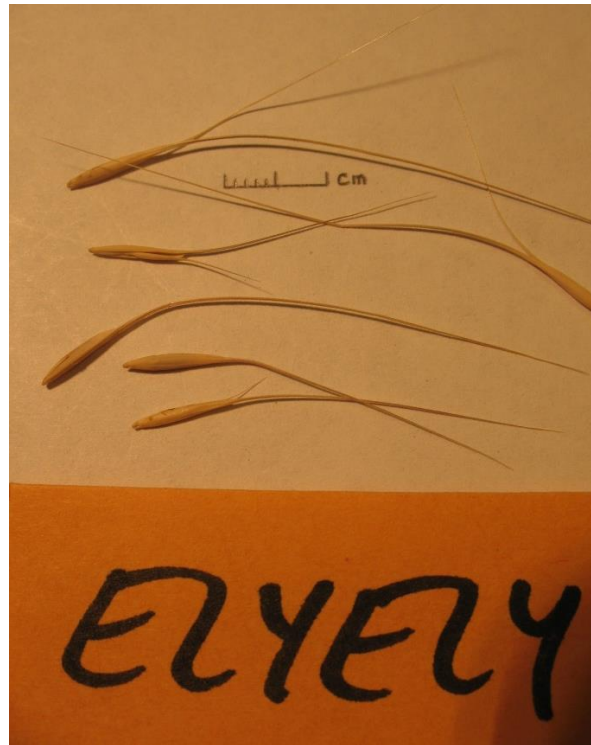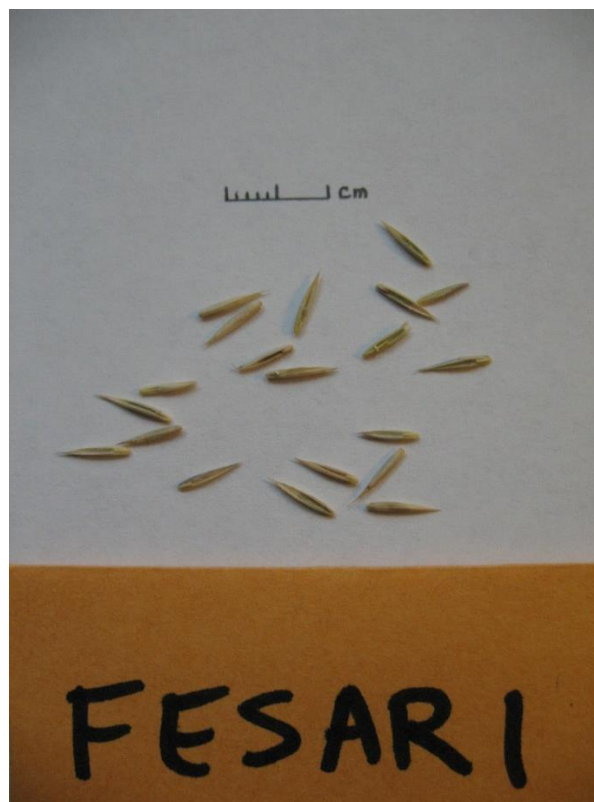
Figure A.1. Image of *Bouteloua gracilis* seed. Photo credit: D. Laughlin, 2008.

Figure A.2. Image of *Carex geophila* seed. Photo credit: D. Laughlin, 2008.
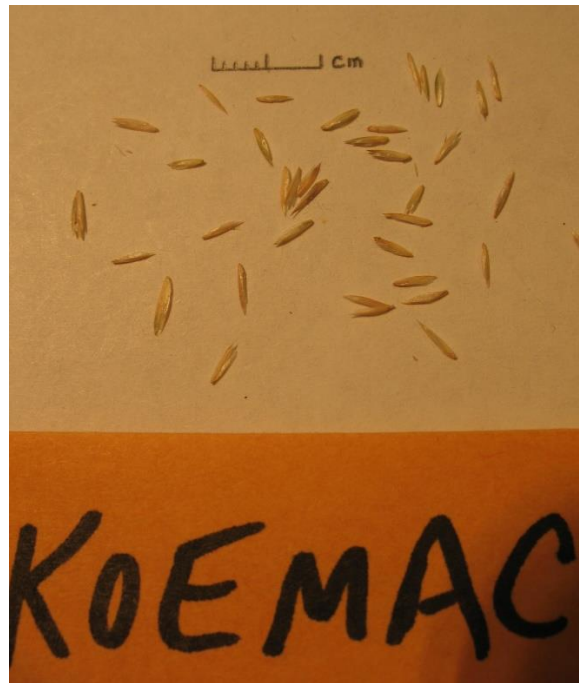
Figure A.3. Image of *Elymus elymoides* seed. Photo credit: D. Laughlin, 2008.
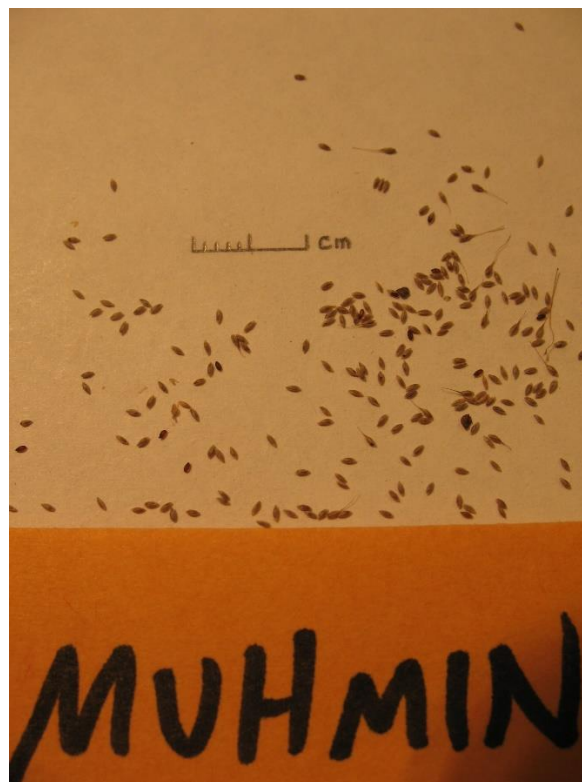

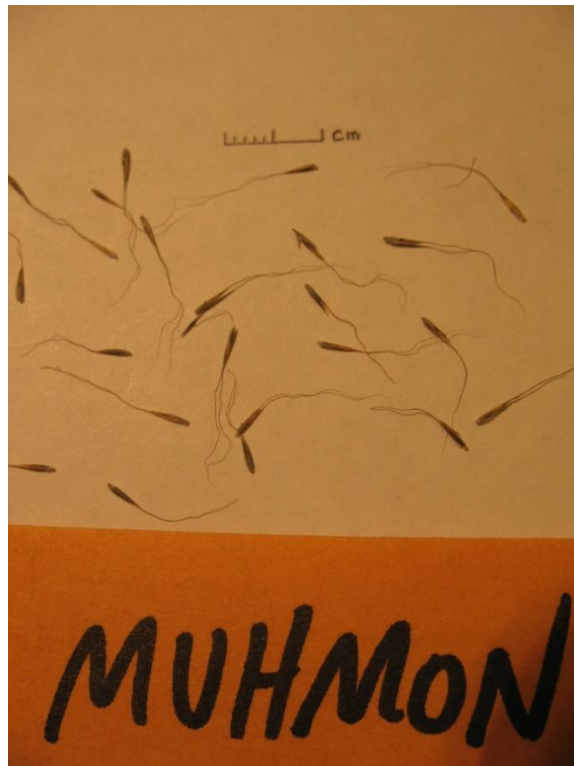**Figure A.4.** Image of *Festuca arizonica* seed. Photo credit: D. Laughlin, 2008.
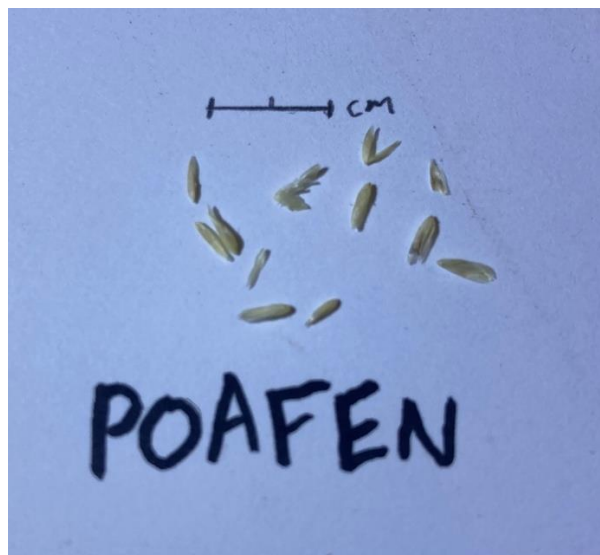
Figure A.5. Image of *Koeleria macrantha* seed. Photo credit: D. Laughlin, 2008.

Figure A.6. Image of *Muhlenbergia minutissima* seed. Photo credit: D. Laughlin, 2008.

Figure A.7. Image of *Muhlenbergia montana* seed. Photo credit: D. Laughlin, 2008.

Figure A.8. Image of *Poa fendleriana* seed. Photo credit: G. Traver, 2022.

Figure A.9. Image of *Sporobolus interruptus* seed. Photo credit: D. Laughlin, 2008.