

UN DECADE ON ECOSYSTEM RESTORATION

RESEARCH ARTICLE

Litter removal reduces seed predation in restored prairies during times when seed predation would otherwise be high

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Understanding patterns of seed predation in tallgrass prairie restorations is vital because seed additions are often used by managers to increase diversity and promote native species. However, the success of seed additions depends on the extent of seed predation. It is not clear how seed predation varies through time and to what extent it is affected by various commonly used management techniques in grasslands (e.g. spring or fall prescribed burns, mowing). We examined how predation of *Sorghastrum nutans* seeds changed during eight trials between June 2018 and April 2019 in plots that received one of four different plant litter removal treatments (fall mow, fall burn, spring burn, and unaltered control). Granivory varied throughout the year, reaching its peak in the late fall and early winter. However, we found that seed predators consumed significantly fewer seeds when litter was removed following fall burn and fall mow treatment applications. These treatments occurred during times when granivory was otherwise high in areas where litter remained intact (control and spring burn plots). Our findings highlight the importance of management decisions and how they interact with granivory in grassland restorations. Both time of year and litter cover determine seed predation rates; seed predators consume more seeds when seeds are abundant but rely on intact litter cover while foraging. This suggests that if seeds are added during the fall, litter should be removed to minimize the loss of seeds to granivory. Alternatively, seed additions during the spring are likely to experience lower rates of seed predation.

Key words: litter removal, prairie restoration, prescribed fire, seed predation, tallgrass prairie

Implications for Practice

- Applying management techniques that remove accumulated plant litter like burning or mowing reduces predation of native seeds when granivory rates are high in the fall and winter.
- Prairie restoration managers wishing to add native seeds when granivory levels are uniformly low may sow seeds in the spring, but may need to artificially cold-stratify seeds. If seeds are added in the fall, sowing should be accompanied by a litter removal treatment to reduce observed high rates of granivory in the late fall and early winter.

Introduction

Ecological restoration is critical for reinstating biodiversity in disturbed, fragmented, and degraded environments (Suding 2011; Wortley et al. 2013). For example, native tallgrass prairie ecosystems have been reduced to 3–5% of their original 162-million hectare range by anthropogenic disturbance and conversion to agriculture (Samson & Knopf 1994) due to their nutrient-rich soil ideal for cultivation (Hoekstra et al. 2005). Very little tallgrass prairie remains intact, often existing only in small and isolated patches that have higher local extinction of native species and colonization

of non-native species (Alstad et al. 2016), as well as decreased ecosystem functioning and services (Pimentel et al. 1997). Restoring degraded tallgrass prairie habitats with active management is vital to preserving biodiversity and reducing invasion by exotic plant species (Hobbs & Cramer 2008; Trowbridge et al. 2017). Prairie managers have tested and employed many different management techniques, including transplanting prairie sod and native plant seedlings (Middleton et al. 2010), reintroducing native ungulate grazers (Martin & Wilsey 2006), sowing target species with

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chemical coatings to deter predators and increase seed establishment (Pedrini et al. 2020), and prescribing controlled fire (Brockway et al. 2002). Despite the importance of active restoration efforts in prairie ecosystems, we still do not know how the type and timing of management activities interact to influence restoration success.

Because successful plant recruitment is an essential part of prairie restorations, management efforts often focus on sowing native seeds onto old fields and degraded habitats (Applestein et al. 2018; Larson et al. 2018). However, because there are many taxa that consume seeds in prairies, including rodents (Howe & Brown 2000; Bricker et al. 2010), birds (Howe & Brown 1999), and insects (Crist & MacMahon 1992; Linabury et al. 2019), the efficacy of seed additions may depend strongly on granivory levels (Archer & Pyke 1991; Orrock et al. 2009). Maximizing the effectiveness of seed sowing efforts and native plant recruitment in tallgrass prairie restorations depends upon considering how granivore foraging responds to applied management techniques. Seed predators often select larger and more nutritious seeds (Mittelbach & Gross 1984; Hoffman et al. 1995; Maron et al. 2012) and prefer native prairie species regardless of relative abundance (Schneider et al. 2017). Seed limitation through selective predation reduces native seedling emergence and plant recruitment in restorations (Howe et al. 2006). Quantifying the impacts of seed predation and developing strategies to minimize seed loss due to granivores can save on expensive native seeds (\$3,600–5,000/ha) and increase restoration success (Pellish et al. 2018).

Many factors, including habitat structure, environmental cues, and abiotic variables are known to modulate how granivores forage and the amount and types of seeds that they consume (Manson & Stiles 1998). The timing and type of management efforts may also affect granivory, especially if treatments alter microhabitat structure (Orrock et al. 2004). Fire and other management methods may impact seed predation by removing litter (dead plant material) that granivores must navigate when searching for seeds (Kaufman et al. 1989; Facelli & Pickett 1991). However, results of litter removal effects on seed predation have been contradictory. Using fire (or similar techniques, such as mowing) to remove plant litter may increase granivory by allowing for unrestricted foraging and making seeds easier to locate (Clark et al. 1991; Reed et al. 2004). Conversely, removing litter may decrease seed predation because rodent granivores prefer to avoid predator encounters by foraging under vegetative cover (Kotler et al. 1991; Orrock et al. 2004; Fanson 2010). Seed predation can also vary as granivore populations fluctuate throughout the year (Brady & Slade 2004) and plant phenology changes during the growing season (Rabinowitz & Rapp 1980). Despite the importance of granivory in prairie restorations and previous experiments that show how management efforts affect seed predation levels, we do not know how different forms of management affect seasonal patterns of granivory. Determining the optimal time of year to add seeds when they are most likely to survive and successfully germinate can increase restoration effectiveness and help managers to avoid seeding at disadvantageous times when higher proportions of seeds are lost to granivory.

Examining how common management techniques that alter litter levels impact the amount of native seed predation in prairie restorations can inform managers on how their methods affect granivore foraging and possibly the success of seed addition efforts. While many studies have used seed addition and seed predation trials to quantify how granivore foraging is impacted by environmental variables, such as litter depth and fire timing, trials are usually only conducted during the growing season (spring-fall), and rarely over the course of a year. We are aware of only one other study (Schneider et al. 2017) that has conducted seed predation trials throughout an entire year to assess granivore foraging patterns of native seeds in restorations. To better understand how seed predation is affected by management treatments across all seasons, we measured seed predation over 1 year in a restored tallgrass prairie subjected to four different management techniques. We examined how seed predation changes through time, and how management techniques that reduce litter at different times of the year affect seed predation. We expected that seed predation would be highest in the fall, when seeds are most abundant, but that litter removal would decrease seed predation levels immediately after treatment applications because seed predators prefer to forage under litter cover. These results will help managers determine which prairie restoration methods maximize the establishment of sown seeds by considering the role of litter removal timing on seed predation.

Methods

Study Site

Our study was conducted at Mounds View Grassland, a 572-acre area in southern Wisconsin (42.955027°N, 89.861428°W) under the management of the Prairie Enthusiasts (<https://www.theprairieenthusiasts.org/>). Restoration of the study plots began in the fall of 2011 with the seeding of native species onto corn stubble. The current community consists of common Midwest tallgrass prairie species (e.g. *Andropogon gerardi*, *Asclepias syriaca*, *Silphium integrifolium*, *Sorghastrum nutans*) and has an average vegetation height of 92 cm with continuous vegetation cover (Henn 2020). The area is characterized by driftless region topography and ecology (Davis 1977), and dry to mesic soil. A complete description of the study site can be found in Henn (2020).

Experimental Design

In 2016, we established an experiment where four different management techniques were applied annually; fall burn, fall mow, spring burn, and an unaltered control. These treatments vary in the timing of litter removal and whether the fire is applied. We established eight blocks, each consisting of four treatment plots (10 × 20 m) to which we randomly assigned the management treatments (Fig. 1). Plots were separated by a 3-m wide buffer that was mowed each fall to act as a fire break (Henn 2020). In the 2018–2019 season, the third year of treatment applications, the fall mow was conducted on 29 October, 2018, the fall burn

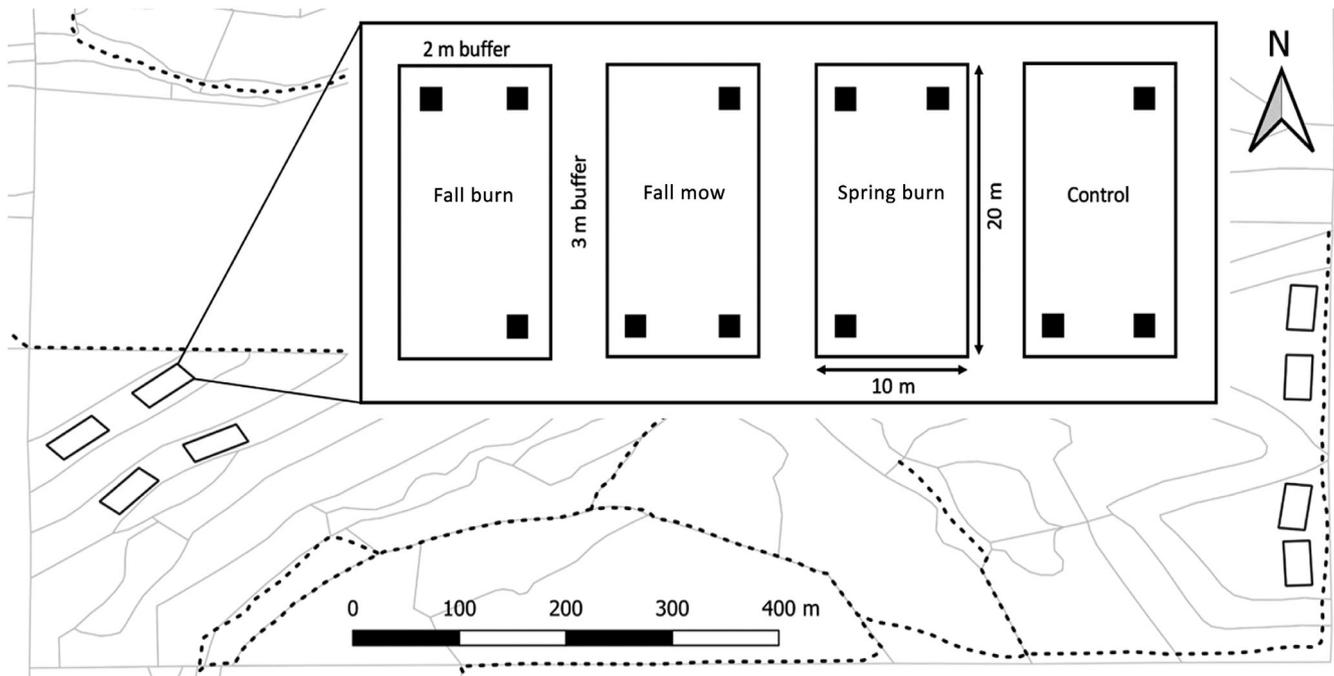


Figure 1. Map of our study site, Mounds View Grassland. Light gray lines indicate borders between management units, dotted lines are roads, and dark rectangles are the eight experimental blocks. The inset depicts one experimental block with four randomly assigned treatment plots (spring burn, fall burn, fall mow, and control). Three seed predation trays (black squares) were randomly assigned to three of the four corners of each plot and placed two meters from the edges of the plot.

on 16 December, 2018, and the spring burn on 15 April, 2019. Fire treatments consumed the majority of aboveground plant material. Mowing removed plant material above 8 cm.

Seed Predation Trials

To assess seed removal frequency as impacted by each management technique, we conducted eight seed predation trials over an 11-month period from June 2018 to April 2019 (trial 1: 22 June, 2018–25 June, 2018; trial 2: 6 July, 2018–9 July, 2018; trial 3: 8 August, 2018–11 August, 2018; trial 4: 14 September, 2018–17 September, 2018; trial 5: 14 November, 2018–19 November, 2018; trial 6: 17 December, 2018–21 December, 2018; trial 7: 25 March, 2019–29 March, 2019; trial 8: 22 April, 2019–26 April, 2019). Within each treatment plot, we established seed removal trays that were randomly assigned to three of the four corners of each treatment plot (24 replicates per treatment, for 96 total trays per trial) and located 2 m from plot edges (Fig. 1). Each tray consisted of a plastic storage container (24.13 × 15.75 × 13.46 cm), with two 6.35 cm diameter holes drilled in adjacent sides, tight transparent covers, and affixed to the ground with lawn staples (Orrock et al. 2004). This design allows for rodent and arthropod access, excludes entry of avian seed predators, and greatly reduces seed loss due to wind. Between trials, trays were left in the prairie to allow for native animal species to acclimate to their presence. For seeds predation trials, each tray was filled with 40 locally collected *S. nutans* (Indiangrass) seeds and mixed homogeneously with

250 mL fine-grain sand. Trays were deployed at mid-day and collected 3–5 days later at midday (Table S1). After collection, samples were sieved and remaining *S. nutans* seeds were counted to determine the number of seeds removed. Trays that were found to be disturbed (e.g. tipped over, missing lids, or spilled sand) were not included in the analysis because of possible non-predative seed loss. Evidence of seed predation (rodent scat and empty seed shells) in individual trays was noted as well.

Analysis

To determine how disturbances affected seed predation, we calculated the proportion of seeds consumed at the end of each trial by dividing the number of seeds missing in each tray after the trial by the number of seeds that were deployed at the beginning of the trial. We calculated this value on up to three samples from each treatment plot during each trial, which we pooled together to avoid pseudoreplication. For all analyses, we logit-transformed these proportions to improve model performance.

To answer our question about how seed predation changes through time and whether management treatments affect seed predation, we used a linear mixed effect model that examined the effect of management treatment, trial, and their interaction on seed predation as fixed effects. We fit random intercepts for treatment nested in block, and trial nested in block to account for the blocked, repeated measures structure of this experiment. We conducted Tukey post hoc tests to determine differences between treatments within each trial.

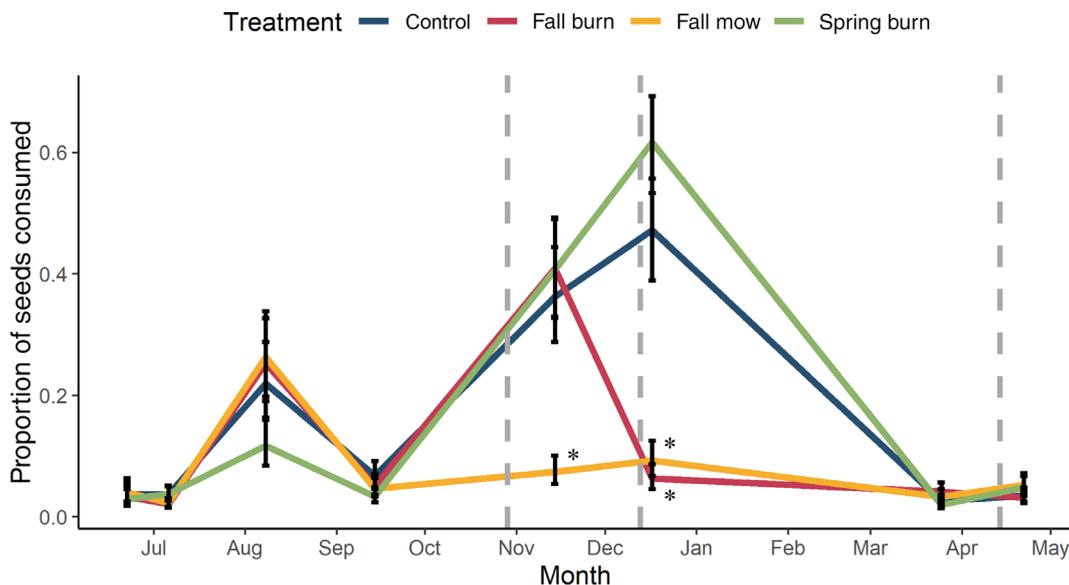


Figure 2. Back-transformed model predictions for proportions of seeds consumed (transformed from logit proportions) in seed trays at end of each trial where higher values indicate more seeds removed. Error bars indicate \pm SE. Dashed vertical lines indicate treatment applications (fall mow on 29 October, 2018, fall burn on 16 December, 2018, and spring burn on 15 April, 2019). Asterisks indicate significant differences between treatment and control plots during that trial (Tukey post hoc test, $p < 0.01$).

Results

Over all trials and treatments, a total of 715 samples were collected, counted, and included in the analysis. We excluded 53 samples that were disturbed during trials. Management treatments, on their own, did not affect seed predation rates ($F = 2.76$; $df = 3, 22.0$; $p = 0.07$; Table S1). However, there was variation in seed predation between trials ($F = 30.98$; $df = 7, 44.4$; $p < 0.001$; Table S1), and this variation depended on management treatments ($F = 5.48$; $df = 21, 134.1$; $p < 0.001$; Table S1, Fig. 2). Most notably, the fall mow treatment significantly reduced predation following the treatment application in October, 2018 (Tukey post hoc test, $p < 0.01$). Likewise, the fall burn treatment experienced significantly less seed predation than spring burn and control plots immediately following burning in December 2018 (Tukey post hoc test, $p < 0.01$). These reductions in seed predation were during times when seed predation was otherwise high in the spring burn and control plots. The spring burn treatment did not result in any significant differences from the control plots.

Discussion

Seed survival is essential to the success of prairie and grassland restoration (Foster & Tilman 2003; Orrock et al. 2009; Alstad et al. 2018). However, uncertainty about how seed predation differs as a function of management context and the timing of seed additions can hamper our ability to implement optimal restoration seeding to promote native plant recruitment. Our results show that management context affects seed predation during specific times of the year, linking management efforts that reduce build-up plant litter with the timing of seed additions.

Moreover, our study suggests that changes in litter levels and the time of year when managers add seeds both interact to influence seed predation, as granivores preferred to forage in areas with intact litter cover only during times of year when seeds are a large part of their diet.

Our experiment revealed that litter plays a key role in affecting granivory in a restored tallgrass prairie, supporting our hypothesis that seed predation levels would decrease immediately after treatment applications that reduced litter. Both fall fire and mowing treatments in our study were effective at reducing granivory levels by eliminating litter during the late fall and early winter when native seeds are preferentially selected by rodents (Schneider et al. 2017). However, the granivory reduction was only evident immediately following the fall treatments, and we did not observe any reduction of predation for any treatment during other times of the year, suggesting that treatment effects are only consequential in the season that they are applied. While the spring burn also removed built-up plant litter, it was during a time when native rodents preferentially consume emerging green plant shoots over seeds, resulting in lower spring seed predation levels in all treatments (Grant & Birney 1979; Lindroth & Batzli 1984). Our results are consistent with those from an Ontario prairie where granivory increased during the same time periods (May–July, November–January), when native seed production is high in the mid-summer, and when other food sources are scarce in the early and middle parts of winter (Schneider et al. 2017). This seasonal pattern of seed predation may be generalizable to other grassland and prairie systems, and could inform restoration managers wishing to plan seed additions when local granivores are eating fewer native seeds.

Restorations are often limited by the cost and availability of seeds and prairie granivores may hamper seeding efforts with

selective seed predation throughout the year. Thus, managers may increase the cost-effectiveness and success of seed additions by seeding in the spring when granivory is lower overall across management treatments. However, seeds added in the spring might have to be artificially cold stratified (kept in dark, near-freezing conditions for several months) or treated with compounds (e.g. gibberellic acid) to break seed dormancy and ensure that germination occurs after sowing (Barak et al. 2018). If seeding in the spring, managers should consider the cold stratification needs of each seeded species (Baskin & Baskin 2020) since cold stratification needs differ based on phylogenetic and functional trait differences (Barak et al. 2018). Alternatively, seeds can be added in the fall and allowed to cold-stratify naturally if sowing is accompanied by litter reduction to reduce observed high rates of fall and winter granivory. Mowing during the growing season has also been shown to foster forb seedling recruitment success by increasing light and soil availability, as well as reducing overwintering seedling mortality (Williams et al. 2007). Since mowing and burning in the fall both resulted in reduced seed predation, mowing may be a viable option for restoration managers when burning is not available.

Overall, both the time of year of seed additions and levels of litter in management treatments had important interactive effects on granivory levels in this tallgrass prairie restoration. Our study is particularly relevant and useful to prairie restorations because we tested the influence of four different management techniques across multiple seasons on seed predation, a widespread driver of seed loss (Collins et al. 1998; Rowe 2010). Investigating the direct and combined effects of treatment applications with seasonal and abiotic variables allows for a better understanding of the dynamics that influence the success of often-costly restorations. Future studies are needed to evaluate the effects of other factors on seed predation in restorations, such as nocturnal foraging conditions, the species, and qualities of targeted native seeds, and the dynamics and local history of prairie restoration sites. Previous experiments have documented that nocturnal foraging conditions often have a large influence on rodent granivores (Orrock et al. 2004), including the amount of moonlight (which has an inverse relationship with seed predation levels) and precipitation, both of which serve as indirect cues for rodents to determine predator risk when foraging. We also used one model prairie species, *Sorghastrum nutans* (Indiangrass), as an indicator for overall native seed predation, but granivores may alter their predation levels throughout the year if other native species of seeds are provided (Schneider et al. 2017). Seed predation may also vary by site-specific features, such as agricultural land-use history and the existing rodent population (Reed et al. 2006); therefore, granivores may have different responses to plant litter and the timing of seed sowing depending on previous land-use history, fire frequency, and habitat patchiness (Morris & Davidson 2000; Stuhler & Orrock 2016). Increasing seedling recruitment through supplemental seeding is often required for restoring native species diversity and richness and decreasing sowed seed loss is a vital yet complicated part of increasing restoration success and longevity (Carter & Blair 2012; Trowbridge et al. 2017). Managers considering how to reduce seed mortality through granivory could

incorporate litter removal techniques and sow seeds in the fall when granivory levels are high, or add cold-stratified seeds in the spring when granivory levels are low.

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Supporting Information

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

Table S1. Analysis of variance (ANOVA) table for the linear mixed effect model comparing seed predation.