RESEARCH ARTICLE

Fire as a Site Preparation Tool in Grassland Restoration: Seed Size Effects on Recruitment Success

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ABSTRACT

Plants may either produce a large number of small seeds, or a comparatively small number of large seeds. This widely-observed tradeoff in plant reproductive strategies has important implications for ecological restoration by impacting dispersal, establishment, and competitive success of species. Here, we tested how applying fire to decrease environmental stress impacts the establishment success of species with differing seed sizes in a well-replicated, fully randomized planting experiment. Specifically, seedling establishment responses were compared among four pairs of closely-related plant species (one small-seeded vs. one large-seeded species in each pair), and average seed size among species pairs varied by an order of magnitude (from 0.375 to 9.17 mg). Although overall establishment rates were extremely low (< 1%), we found that large-seeded species established more readily than small-seeded species, and that using prescribed fire in site preparation increased establishment success across all species regardless of seed size. Surprisingly, large- and small-seeded species established equally well in unburned plots, which was contrary to our expectations that large-seeded species would establish more readily than small-seeded species in unburned plots. Perhaps a seed size threshold exists, below which seedlings cannot overcome the stress of leaf litter in unburned plots. This study suggests that preparing a restoration site with prescribed fire prior to seeding will substantially increase the establishment success of seeds sown into existing vegetation.

Keywords: leaf litter, interseeding, prairie restoration, tolerance/fecundity tradeoff

Restoration Recap

- Low rates of native seed establishment can be a barrier for restoration projects, particularly given the high cost of native seeds. Our research aims to improve restoration outcomes by testing whether site preparation requirements vary among individual species as a function of seed size.
- Large-seeded species established at higher rates than small-seeded species.
- Preparing the grassland restoration site with prescribed fire prior to planting increased the establishment success of both large- and small-seeded species.
- Overall establishment rates were extremely low (< 1%), indicating that the seed to seedling transition is a major bottleneck in restoration plantings, and high seeding densities may be required to ensure desired densities of mature plants.

Seed size is a fundamental characteristic of plants that alters processes including seedling survival (Muscarella et al. 2013), germination (Moles and Westoby 2004a), seed predation (Gómez et al. 2008), dispersal ability (Dupré and Ehrlén 2002), and longevity in the soil seedbank (Moles et al. 2000). Early theoretical studies predicted that an optimal seed size should exist for each habitat based on biotic and abiotic conditions (Smith and Fretwell 1974). Empirical tests, however, did not support these expectations, instead finding variation in seed size spanning several orders of magnitude in any given plant community (Leishman et al. 2000).

To help explain the wide variation in observed seed sizes, previous theoretical work proposed a tradeoff between plants that produce many small seeds vs. those

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that produce relatively few large seeds (Geritz 1995, Rees and Westoby 1997). Specifically, these theoretical frameworks proposed a competition-colonization tradeoff, whereby asymmetrical competition led to large-seeded species being able to persist and invade in direct competition with other seeds, while small-seeded species could colonize by finding uncontested germination sites via high seed production. However, studies examining this tradeoff suggest that there is insufficient competitive asymmetry between large and small seeds to maintain the variation in seed size (Coomes and Grubb 2003, Turnbull et al. 2004, Eriksson 2005, Ben-Hur and Kadmon 2015, but see Turnbull et al. 1999), as seedlings rarely compete directly against one another (Moles and Westoby 2004b). Instead, establishment is usually thwarted by competition from adult plants or stress from local biotic or abiotic conditions (Moles and Westoby 2004a, 2004b).

Understanding the fundamental limitations and tradeoffs for seed size variation is especially critical for the restoration of plant communities. Restoration often involves sowing seeds into sites with different environmental conditions and histories (Rowe 2010, Larson et al. 2011). Despite recent advances in restoration ecology, the ability to predict outcomes remains low (Brudvig 2011), with few studies evaluating recovery methods (Rowe 2010). Knowing how seedling establishment rates vary based on seed size and site conditions will help restoration practitioners make strategic decisions about site preparation and seed mix composition. Such knowledge will be particularly relevant for ecosystems such as temperate grasslands that have been heavily impacted by habitat loss and fragmentation (Samson and Knopf 1994, Hoekstra et al. 2004, Briggs et al. 2012).

Recently, a revised framework for understanding seed size tradeoffs and variation was proposed in which the original competition-colonization tradeoff is re-cast as a fecundity-tolerance tradeoff (Muller-Landau 2010). In this model, large seeds are advantageous not because of a competitive advantage, but rather because of a superior ability to tolerate environmental stress. Wide variation in seed size is maintained because large, stress-tolerant seeds successfully establish in harsh germination sites, while small seeds arrive at numerous sites and germinate readily in less stressful locations. This revised framework has not yet been thoroughly tested by empirical studies.

Here, we tested theoretical predictions relating seed size, measured by seed mass, to stress tolerance in the context of tallgrass prairie restoration using a controlled field experiment. We used prescribed fire, a common site preparation technique in grassland restoration, to manipulate the stress of germination sites. We predicted that, 1) large seeds would generally recruit at higher rates than small seeds. Furthermore, following the predictions of the fecundity-tolerance tradeoff, we also expected that, 2) seed size and the burn treatment would interact, such that large seeds would establish well in both burned and unburned sites, whereas small seeds would establish more successfully in burned (i.e., low-stress) sites relative to unburned (i.e., high-stress) sites.

Methods

This study was conducted in Iowa County, Wisconsin, USA (43°1′15.67″ N, 89°57′48.92″ W) in an old field pasture which has a history of grazing but has never been cultivated. At the time the experiment was initiated, dominant cover was from *Bromus inermis* (smooth brome), a cool-season exotic grass. The pasture is approximately one hectare in size, is located on silt loam soil, and has a southeast aspect with an average slope of 15%.

We created a fully randomized experiment with two treatments—prescribed fire (burned or unburned) and seed size (large or small seed within four species pairs)—randomly assigned to each plot. There were 270 1.25-m × 1.25-m plots in total, with 15 replicates per seed size and fire combination, as well as 30 control plots that did not receive any seed addition. We sampled a 0.75-m × 0.75-m plot within the treated area; the 0.25-m treated buffer around the perimeter of the sampled interior controlled for possible edge effects. Plots were separated from one another by 1-m paths. Please refer to Supplementary Figure S1 for further details and a diagram of plot design.

Prescribed fire is a common site preparation technique in grassland restoration, especially when seeds are to be sown into existing vegetation (Rowe 2010). Specifically, fire is thought to reduce stress for seeds and seedlings by removing litter (Copeland et al. 2002, Ruprecht and Szabó 2012), which can limit both seed-soil contact (Zimmermann et al. 2008), as well as photosynthetically active radiation (Egawa and Tsuyuzaki 2013). Plots assigned to the prescribed fire treatment were burned in October, 2013. Burns were contained to single plots using a burn box constructed of plywood lined with aluminum flashing. The burn treatment extended 25 cm beyond the sampled area of the plot to avoid edge effects. We lit fires using a drip torch and completely burned the standing vegetation and accumulated litter; burned plots had significantly more bare soil and less litter compared to unburned plots (Supplementary Methods). We recognize that fire behavior and effects may differ between burns confined to a burn box vs. burns at larger spatial scales. However, this implementation of fire was ideal for our goals of a randomized and well-replicated experimental test of site preparation via prescribed burn, and resulted in clear differences between burned and unburned plots, as outlined in the Supplementary Methods.

To test for the effect of seed size, we selected eight species of native prairie herbs representing a range of seed sizes (Table 1). All eight species were well suited to the site conditions but were not present in the vicinity of the

Table 1. Effects of seed size on establishment success in burned and unburned plots. The experiment included four closely-related species pairs (pairs designated with †), each representing one large- and one small-seeded species. Single species were sown at a rate of 80 viable seeds per 1.25m × 1.25m plot, for a total of 2,400 viable seeds per species across all plots. Seedling count represents total number of established seedlings observed over the first two growing seasons. Asterisks indicate species where establishment was significantly higher in burned plots. The degrees of freedom for all tests was 1, 205.

Species name	Seed mass (mg)	Seed size	Seedling count	F	*p*
†*Solidago nemoralis*	0.12	Small	9	0.66	0.41
†*Solidago rigida*	0.63	Large	11	0.46	0.49
Dalea candida	0.063	Small	3	0.00	1.00
Dalea purpurea	1.43	Large	5	0.88	0.35
†*Lespedeza capitata*	2.86	Small	72	11.39	< 0.01*
†*Desmodium canadense*	6.25	Large	79	2.46	0.19
Amorpha canescens	1.67	Small	9	3.61	0.059
Baptisia alba	16.67	Large	11	0.74	0.39

experiment prior to seed addition. To control for phylogenetic relatedness, we chose closely-related pairs of species with one large-seeded species and one small-seeded species. Each seed addition plot received seeds of a single species. The seeding rate was adjusted for each species such that an equal number of viable seeds were added to each plot. Seeds were broadcast by hand in May 2014. We intentionally completed the seeding immediately prior to several days of gentle rain and do not expect that drought stress was a major impediment to establishment, as the 2014 growing season was consistently wetter than average, with cumulative rainfall between May and October 5.1 cm (7.2%) higher than the 30-year average.

We purchased local-genotype seeds from Agrecol Nursery (www.agrecol.com), and stratified and scarified them in the laboratory according to species-specific recommendations from Baskin and Baskin (1998). We used a germination trial to inform seeding rates such that 80 viable seeds of each species were sown per plot (Supplementary Methods).

Two seasons of post-treatment data were collected in August 2014 and July 2015. For the sown species, we recorded the number of individuals present in each plot post-treatment. During the 2014 sampling, all seedlings were first-year plants; during the 2015 sampling, we recorded the number of individuals of first- and second-year seedlings separately. In each plot, we also recorded the identity and visually estimated the percent cover of all other species present in the plot.

Soil moisture is a major cause of seedling mortality, as young plants are more susceptible to desiccation than older, more established individuals (Moles and Westoby 2004b) and, therefore, an important covariate in our experiment. For each plot, we estimated the soil moisture holding capacity (referred to henceforth as soil moisture), by calculating the proportional difference of dry vs. saturated soil. These methods follow the approach of Salter and Williams (1967), and are fully described by Damschen and Brudvig (2011). In the fall of 2014, we collected a total of four soil samples from the perimeter of each plot, and then combined these samples for a single sample per plot (Supplementary Figure S1).

To determine the effects of experimental treatments on seedling establishment, we used a generalized linear model with soil moisture as a covariate. We used the total number of first year seedlings as our response variable, summing all first-year seedlings recorded in 2014 and 2015. We included fixed effects of fire (burned vs. unburned) and seed size (small vs. large) as binary predictor variables and soil moisture as a continuous covariate. To account for phylogenic relatedness, we nested seed size within species pair (Table 1). Model interpretation did not change if species pair was treated as a fixed or random effect; results presented here are from the model treating species pair as a fixed effect. We also included all pairwise interactions between explanatory variables in the model and the three-way interaction between soil moisture, fire, and seed size. To assess the interaction between seed size and fire, we assessed the difference in establishment between burned and unburned plots for each sown species independently using the "slice" procedure in SAS, which partitions the least squares mean of an interaction to reveal the simple effects.

To avoid the high type I error rates associated with count data in a generalized linear model framework (e.g., poisson or negative binomial distribution, Ives 2015), we log transformed all count-based response variables in our analyses. All analyses were conducted using SAS version 9.4 (SAS Institute, Cary, North Carolina). For all statistical tests $\alpha = 0.05$.

Results

Large-seeded species produced more seedlings after two growing seasons than did closely related small-seeded species (Table 2, Figure 1). Among all four species pairs, the large-seeded species established at a higher rate than the small-seeded species did. Seedling establishment was higher in burned plots than in unburned plots and negatively related to soil moisture (Table 2, Figure 2).

Table 2. Results from the generalized linear model testing effects of soil moisture, fire treatment, and seed size on seedling establishment in a Wisconsin pasture. The response variable in our model was the log transformed count of first year seedlings summed across the first two growing seasons post treatment.

Factor	DF	Type III SS	Mean Square	F	p
Model (r^2 = 0.49)	31, 205	—	—	6.47	< 0.0001
Soil moisture	1	0.75	0.75	18.39	< 0.0001
Fire	1	0.46	0.46	11.16	0.001
Seed size	7	1.83	0.26	6.37	< 0.001
Soil moisture × Fire	1	0.36	0.36	8.83	0.0033
Soil moisture × Seed size	7	1.07	0.15	3.73	0.0008
Fire × Seed size	7	0.51	0.07	1.78	0.092
Fire × Soil Moisture × Seed size	7	0.46	0.07	1.60	0.14

The hypothesized interaction between fire and seed size was detected as a trend, but was not statistically significant across all species (Table 2, Figure 1). One species pair supported this hypothesis (*Lespedeza/Desmodium)*, with higher establishment success of the small-seeded species in the burned plots (Table 1), while the large-seeded species of the pair was unaffected by the fire treatment (Figure 1). A second species pair (*Amorpha/Baptisia*) showed similar trends in establishment (Figure 1), but the interaction was not statistically significant (Table 1). The remaining two species pairs, *Solidago* spp. and *Dalea* spp., did not show any evidence of an interaction (Figure 1). However, we note that low establishment rates for both pairs (only 8 *Dalea* spp. and 20 *Solidago* spp. seedlings established across all plots; Table 1) make discerning any trend for these species difficult. In fact, overall seedling establishment was rare. Of the 19,000+ seeds sown into the experimental plots, only 167 were observed as established seedlings in the first growing season, and 75 in the second growing season. The 75 seedlings detected in the second growing season included 32 first-year plants that did not establish in the first growing season and 43 second-year plants that survived following establishment in the first growing season.

Interestingly, while our hypothesized interaction between fire and seed size was only a trend, the two other two-way interactions between fire and soil moisture and between seed size and soil moisture were both significant (Table 2). The generally negative relationship between seedling establishment and soil moisture was stronger for large-seeded species relative to small-seeded species (Figure 2A) and for burned plots relative to unburned plots (Figure 2B).

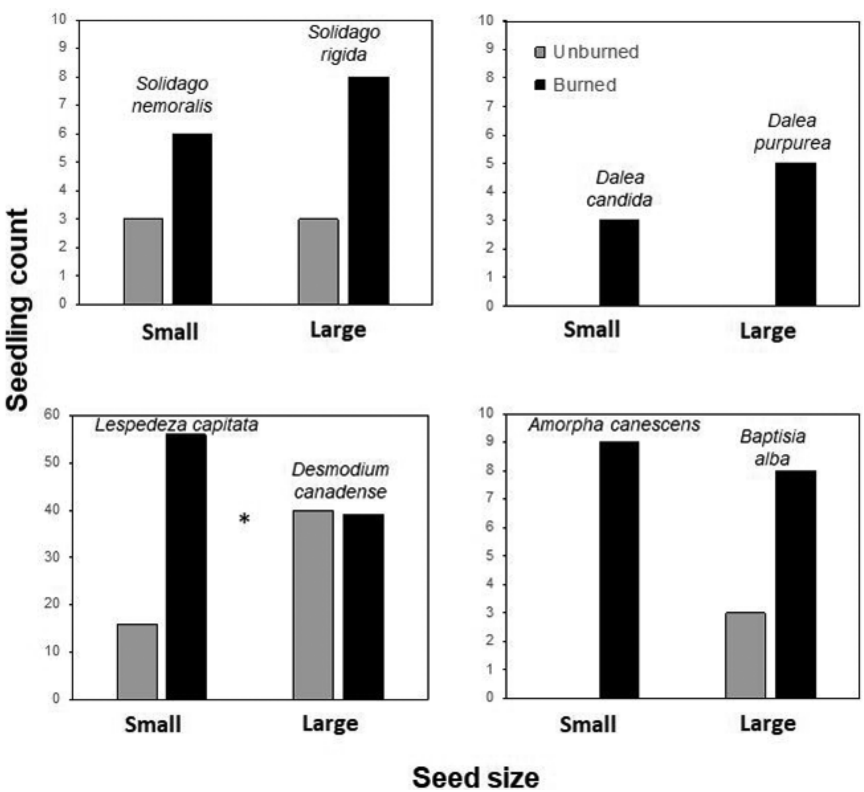

Figure 1. Effects of fire and seed size on seedling establishment in four pairs of closely-related prairie species, Wisconsin, USA. Seedling count represents total number of first-year seedlings summed across all experimental plots in 2014 and 2015. The asterisk indicates the species pair with a statistically significant interaction of seed mass and burning on seedling establishment. Small-seeded species are listed first in each species pair. Note that the y-axis scale for *Lespedeza capitata* and *Desmodium canadense* is substantially larger than the other three panels.

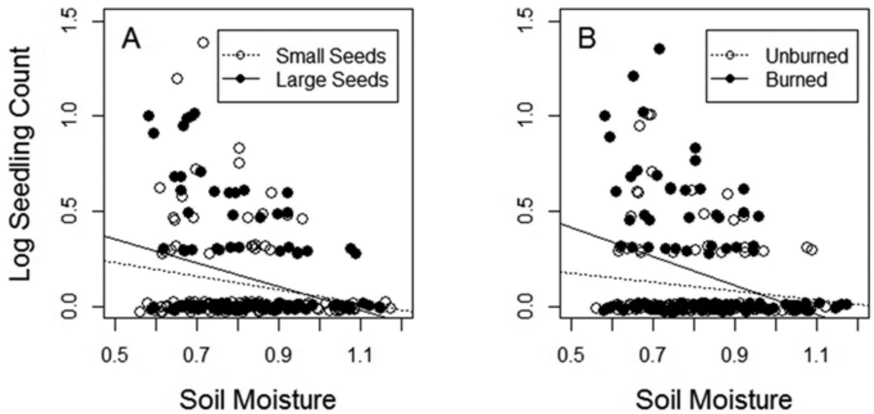

Figure 2. Effects of fire and seed size on seedling establishment across a soil moisture gradient. Soil moisture was measured as the proportional difference between dry and saturated soil. Log seedling count represents number of seedlings of planted species detected in each plot. A) Soil moisture and seed size (where seed size represents nested pairs of closely-related species) significantly interact to determine seedling establishment, as do B) soil moisture and prescribed fire (Table 2).

Discussion

Following the predictions of the tolerance-fecundity trade-off (Muller-Landau 2010), we expected to find an interaction between seed size and our fire treatment such that burning plots prior to planting would disproportionally benefit small-seeded species by removing litter, while large-seeded species would establish equally well in burned and unburned plots. Such a result would have been consistent with a previous body of literature indicating that large seeds are more likely than small seeds to establish despite environmental stress created by accumulated leaf litter (Jakobsson and Eriksson 2000, Muscarella et al. 2013, Lönnberg and Eriksson 2013, but see Ruprecht and Szabó 2012, Egawa and Tsuyuzaki 2013), standing biomass (Burke and Grime 1996), shade (Pearson et al. 2002), and heat shock (Ribeiro et al. 2015). Our results, however, were mixed. In our overall model, this hypothesized interaction was detected only as a trend. Of the four species pairs, the establishment of one pair (*Lespedeza/Desmodium*) supported the hypothesized interaction, while the other three pairs (*Amorpha/Baptisia, Solidago* spp. and *Dalea* spp.) did not. It is important to note that for the latter three species pairs, low overall establishment rates and, in the case of *Dalea*, not a single successful case of seedling establishment in an unburned plot, limit the statistical inferences that can be drawn.

One possible explanation for our mixed results regarding the hypothesized interaction between fire and seed size is that an overall seed size threshold exists. When considering all eight species individually (i.e., not treating seed size as nested), the four species with the largest seeds either supported the hypothesis (*Lespedeza/Desmodium*) or showed supportive trends (*Amorpha/Baptisia)*, while the four smallest seeded species showed no evidence of an interaction between burn treatment and seed size. Perhaps, below such a threshold, even the "large" seeds within each of our pairs were not large enough to confer the ability to overcome the stress of leaf litter in unburned plots. Such a threshold is consistent with the complete failure of *Dalea*, one of our smallest seeded species pairs, to establish in the unburned plots. We are not aware of studies testing a sufficient range and number of seed sizes to evaluate this possible threshold, but this may be a promising avenue for further research.

The existence of a threshold could be related to accumulated litter, which influences a number of processes related to seed and seedling survival. For example, small seed size is correlated with high light requirements for germination (Milberg et al. 2000, Jensen and Gutekunst 2003). As a result, small seeds could be more strongly affected by the limited light conditions associated with litter than large seeds are. Alternatively, once a seed disperses, litter can prevent germination by trapping seeds above the soil surface (Ruprecht and Szabó 2012, Egawa and Tsuyuzaki 2013). However, while litter generally decreases seed germination, it may actually increase seedling establishment. For example, litter may facilitate establishment by buffering against drought (Facelli and Pickett 1991, Eckstein and Donath 2005, Carrington 2014), which is an important source of seedling mortality following germination (Moles and Westoby 2004b).

Sites can be stressful in a variety of ways, and in this study, we manipulated stress levels using prescribed fire. Our rationale was that by removing litter (Copeland et al. 2002, Ruprecht and Szabó 2012), fire would increase both seed-soil contact (Zimmermann et al. 2008), as well as photosynthetically active radiation (Egawa and Tsuyuzaki 2013), thus ameliorating two barriers to seed germination and establishment. Furthermore, fire represents both a natural disturbance in this ecosystem (Briggs et al. 2012) as well as a common site preparation technique in grassland restoration projects (Rowe 2010), and thus was a logical experimental treatment. However, we recognize that fire may have numerous impacts on germination and establishment success beyond removal of litter, including altered biotic (e.g., plant-animal interactions (Knight and Holt 2005), plant growth rates (Johnson and Matchett 2001)) and abiotic (e.g., volatilizing soil nitrogen (Anderson et al. 2006), increasing soil temperature (Vermeire et al. 2005)) conditions. As a result, we acknowledge that the results of this field study should be interpreted not as a pure test of stress per se, but rather as an examination of seedling recruitment in grasslands with relevance for both ecological theory as well as applied restoration practice.

Fewer than one percent all of the seeds sown into our experimental plots were detected as established seedlings in the two seasons following seed addition, further demonstrating that the seed to seedling transition is a major bottleneck for plants (Muscarella et al. 2013). Other grassland seeding experiments suggest a strong role of recruitment limitation (i.e., limited propagule availability) when seeds are sown into existing vegetation (Carrington 2014, Tilman 1997, Foster and Tilman 2003). The challenge of low seedling establishment success is compounded by extreme loss of habitat in this system, leaving prairie grassland patches small and isolated from each other (Alstad and Damschen 2015) thereby making the chances of successful propagule dispersal among patches vanishingly small.

We found moderate evidence that large seeds established more readily than small seeds did, and strong evidence that reducing the stress of the germination site with a litter-removing prescribed fire increased establishment. Our experiment produced equivocal evidence that seed size and fire interact; had this hypothesized interaction been clearly supported by our data, it would have suggested that burning a restoration site prior to planting would especially favor small-seeded species. While we did not document strong evidence for this disproportional benefit to small seeds, we did find that the establishment success of native forb seeds planted into existing vegetation is substantially increased with a pre-planting burn. We sowed seeds of grassland species directly into the sward of an old-field pasture, where accumulated litter from previous growing seasons and soil moisture levels represented significant barriers to seedling establishment. These results are particularly relevant to grassland restoration projects using similar interseeding techniques (i.e., planting into existing vegetation), because of similarity in dominant stresses. Our study suggests that successful outcomes for interseeded prairie restorations will require high seed densities, and be aided by preparation techniques (e.g., prescribed fire) that reduce the site stress prior to planting.

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