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RESEARCH ARTICLE

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Evaluating Seeding Methods and Rates for Prairie Restoration

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ABSTRACT: The demand for restoration of degraded lands to diverse native habitat is growing, requiring efficient strategies for large-scale seeding and planting of native species. Restoration is often limited by low germination and establishment rates of native plants, so identifying the most effective seeding methods and rates may speed the restoration process. We tested three different methods of seeding (broadcasting, drilling, simulated hydroseeding) and five seeding rates (ranging from 0 to 1400 seeds/m²) to determine their efficacy in establishing three common species of Pacific Northwest prairies: *Festuca roemeri*, *Eriophyllum lanatum*, and *Potentilla gracilis*. We sowed seeds into six arrays at three western Washington sites on two dates (January and October) and monitored plant abundance for three years. We found that broadcast and simulated hydroseeding did not produce significantly different outcomes, suggesting that the extra resources required for hydromulching are not necessary. Additionally, broadcast seeding resulted in more consistent and reliable native plant establishment than seed drilling. Increasing seeding rates increased abundance, as expected, but species remained seed limited even at the highest seeding rates. Establishment varied considerably by site and seeding date. First-year establishment was positively correlated to third-year abundance, but this also varied greatly by site and species. Due to temporal and spatial variability in establishment, managers should evaluate treatments on individual sites and monitor results for several years after sowing.

Index terms: broadcast seeding, grassland, hydroseeding, seed drilling, seed limitation

INTRODUCTION

Many plant species are propagule limited (Zobel et al. 2000; Foster and Tilman 2003; Martin and Wilsey 2006; Dickson and Busby 2009). Limited seed availability shapes natural vegetation dynamics, but also influences land management activities. For example, restoration of native plant communities often requires the active seeding or planting of desired species. However, species diversity and seed quantity in restoration seed mixes are often restricted, due to limited production at commercial nurseries (Schultz 2001; Rowe 2010) and limited wild source populations (Meissen et al. 2015), emphasizing the importance of using the available seed effectively. To do so, we must understand how establishment varies among species and seeding methods and identify optimal seeding rates so that plant density objectives are met without wasting seed.

Restoration land managers have increasingly been interested in adapting agricultural seeding methods to restoring degraded prairies (Montalvo et al. 2002; Larson et al. 2011; Mollard and Naeth 2014), especially for large areas (>10 acres) that can benefit from economies of scale. Broadcast seeding, which involves spreading seed over the ground and is sometimes followed by harrowing, is considered standard practice for prairie seeding (Rowe 2010). Seed drilling, which creates shallow (1–2 cm) furrows into which seeds are dropped and then covered, has long been used in post-fire rehabilitation of arid sage-scrub lands and prairie restoration in the midwestern United States (Doerr et al. 1983; Thompson et al. 2006; Larson et al. 2011), but this method has become less commonly used in prairie restoration (Rowe 2010). Seed drilling improves germination of some grass seeds, which are photoinhibited by sunny and dry conditions (Mollard and Naeth 2014). The initial germination benefits of seed drilling may be lost, however, during the seedling establishment phase when there can be intense intra- and inter-specific competition between plants in furrows (Bakker et al. 2003). Hydroseeding, spraying seed in a slurry mixed with mulch, has often been used for roadside stabilization and post-fire rehabilitation. Hydroseeding is effective for erosion control but does not provide ideal seed–soil contact, due to the coating and suspension of the seeds by the mulch slurry and can sometimes be cost prohibitive (Brown and Rice 2001). Besides work by Montalvo et al. (2002), very little research has been done on the effectiveness of hydroseeding for prairie restoration.

Previous research on seeding in degraded prairies indicates that field germination rates are often extremely low and that substantial amounts of seed must be sown to overcome competition from established plants (Maret and Wilson 2000; Wilson et al. 2004; Carter and Blair 2011; Holl et al. 2014). However, recommended seeding rates for grassland restoration can vary greatly and are not always based on field testing. The amount of seed needed to achieve restoration goals may be affected by site conditions, the timing of seeding, and seed viability (Bakker et al. 2003; Larson et al. 2011). Thus, it is important to evaluate rates under different environmental conditions to provide robust guidance for land managers seeking to meet restoration needs without wasting seed.

Restored systems are dynamic, and the effectiveness of both sowing method and rate may change over time. A large number of environmental pressures exist in a newly restored system, and first-year responses may not reflect long-term success (Carter and Blair 2011; Willand et al. 2013). For example, grasses may outcompete forb species over time if seeded at too high a rate (Dickson and Busby 2009). Furthermore, overall species diversity and the abundance of sown species tend to decline over time (Carter and Blair 2011; Török et al. 2011; Willand et al. 2013). Assessing results over multiple years allows for evaluation of perennial plant establishment (defined here as survival to three years) and may be long enough to notice preliminary competitive pressure of graminoids on forbs (Camill et al. 2004). Additionally, documenting if and how establishment varies among sowing treatments and sites over time will provide a better understanding of the mechanisms driving community trajectories for the restored system. This may also enable managers to conduct follow-up treatments (e.g., targeted overseeding with a high density of forbs in sites with high competitive pressure from native grasses) to achieve restoration objectives (Török et al. 2011).

Much of the research on the use of mechanized sowing techniques for prairie restoration has focused on the rehabilitation of former agricultural sites (e.g., Jackson 1999; Montalvo et al. 2002; Bakker et al. 2003; Larson et al. 2011). Our study is among the first to test different methods of mechanized sowing in the restoration of degraded cool-season bunchgrass prairies. Our study area is the south Puget Sound prairie landscape in western Washington, an endangered ecosystem that has lost approximately 92% of its historical range (Crawford and Hall 1997). We focused on sowing Roemer's fescue (*Festuca roemeri* Pavlick. Alexeev), hereafter *Festuca*, Oregon sunshine (*Eriophyllum lanatum* Pursh. Forbes), hereafter *Eriophyllum*, and slender cinquefoil (*Potentilla gracilis* Douglas ex. Hook), hereafter *Potentilla*, for this project because they provide important structural and functional resources for endangered prairie wildlife species and they represent different growth forms (graminoid, rhizomatous forb, and caespitose forb, respectively). We addressed three questions: (1) Which seeding method (drilling, broadcasting, or hydroseeding) is most effective at establishing prairie species? (2) What is the plant establishment response based on seeding rate across sites, seeding dates, and seeding methods? (3) Are first-year metrics good indicators of future abundance?

METHODS

Study Sites

This study was conducted at three grassland sites in western Washington state, USA. Research sites are degraded remnant prairies that are part of large-scale restoration efforts to prepare sites for rare butterfly reintroduction. All sites experienced fire exclusion over the past 150 y (Hamman et al. 2011) and varying levels of nonnative grass and shrub invasion. Glacial Heritage Preserve (46°52'N, 123°3'W) is owned by Thurston County and has a history of invasion by Scotch broom (*Cytisus scoparius* L. Link), a nonnative, nitrogen-fixing shrub that excludes most native prairie species and can alter the soil chemistry and biology (Haubensak and Parker 2004). Tenalquot Preserve (46°54'N, 122°44'W) is owned by The Nature Conservancy and was grazed by horses in the 1990s, which promoted invasion and establishment of weedy nonnative pasture grasses, such as *Arrhenatherum elatius* (L.) P. Beauv. ex J. Presl & C. Presl, *Holcus lanatus* L., and *Anthoxanthum odoratum* L. (a primary component of hay mixtures). Scatter Creek Wildlife Area (46°50'N, 122°59'W) is owned by the Washington Department of Fish and Wildlife and has a combination of grass and shrub invasion and additional ongoing disturbances associated with public access (spread of invasive species by dogs, horses, etc.). Sites are located within 40 km of each other. Mean annual precipitation in this area is approximately 1250 mm, with 75% occurring between October and March (Thurston County Environmental Monitoring 2014). Soils are primarily classified as the Spanaway-Nisqually complex and Spanaway gravelly sandy loam; they are derived from glacial outwash and are deep and well drained (NRCS 2013).

Experimental Design and Setup

The study was conducted on two seeding dates (January and October 2010) at each of the three sites, for a total of six arrays. Prior to seeding, we treated arrays using standard restoration methods developed for prairies in this region (Stanley et al. 2008): we applied a grass-specific herbicide in the spring, burned in the fall, and then applied glyphosate, a broad-spectrum herbicide, within 2 wk of the burn to kill nonnative forbs and grasses that germinated or resprouted after the burn.

In each array, we used a factorial design to test combinations of three seeding methods (drilling, broadcasting, hydroseeding) and five seeding rates (total densities of 0, 350, 700, 1050, and 1400 seeds/m^2). We randomly applied each treatment combination to three replicated strips per array that were on average 129 m^2 in area (size slightly varied among sites). Strips were wide enough to facilitate the use of large seeding equipment. In total, the experiment included 270 strips (6 arrays × 3 blocks per array × 3 seeding methods × 5 seeding rates).

Drill seeding was conducted with a Kasco no-till seed drill (Kasco Manufacturing, Shelbyville, Indiana, USA), sowing seeds at a depth of 1–2 cm and then "closing" the furrows with a soil packer. A Trillion broadcast seeder (Truax Company, New Hope, Minnesota, USA) was used for the broadcast and hydroseed treatments. Broadcast plots were raked with a harrow after seeding. It was not feasible to use a conventional hydroseeder in these arrays due to concerns about seed loss in the corrugated piping and the tank, so we simulated this treatment by spraying Hydrostraw mulch at the standard rate of 2240 kg/ha after broadcast seeding.

The standard seeding methods for prairie restoration in this region involve sowing in October or November, just as the autumn rains are beginning. Our first seeding occurred in January 2010 because high precipitation in November 2009 (30.5 cm) was followed by a 10-day freeze in December (PRISM Climate Group 2015), making the soil extremely unsuitable for supporting heavy seeding equipment. Our second seeding occurred in October 2010; for simplicity, hereafter we refer to the seeding dates by their month. The species mix varied among dates; in January, we used a 0.75:1 mix of *Festuca* and *Eriophyllum.* In October, we used a 3:1:1 mix of *Festuca*, *Eriophyllum*, and *Potentilla.* Ratios were determined by seed weight, which was calculated based on number of seeds per gram for each species. Additionally, on each seeding date we used seed produced during the previous growing season to avoid potential loss of viability with long-term seed storage.

Vegetation Sampling

We monitored the abundance of each sown species and the occurrence of all other species in five 1 × 1 m quadrats distributed along the central axis of each strip. We did not distinguish established individuals from new seedlings, as abundance of established plants was low and fairly consistent across sites (Hamman, pers. obs.) and it was not possible to distinguish young vs. old individuals beyond year one. We recorded abundance one, two, and three years after seeding. For *Festuca* and *Potentilla*, we recorded abundance as the number of individual plants within each quadrat. For *Eriophyllum*, we recorded abundance as number of individual plants in 2010 and 2011 (first- and second-year monitoring for January seeded plots, first-year monitoring for October seeded plots), but as percent cover in 2012 and 2013 (third-year monitoring for January plots, second- and third-year monitoring for October plots) because the rhizomatous growth of this species made it impossible to distinguish individual plants as they progressed from seedling to adult. We estimated percent cover using classes (0%, 0–1%, 1–5%, 6–10%, 11–20%, 21–30%, 31–50%, 51–70%, 71–90%, 91–100%); for analysis, each class was expressed as the midpoint of its cover range.

Data Analysis

We analyzed each combination of species and monitoring year separately. For simplicity, we only report first- and third-year results here; second-year trends were consistent with these results. We began by fitting generalized linear mixed models (glmm) with negative binomial distributions using the R package glmmTMB in R Studio 3.1 with seeded species abundance (density or percent cover) as the response variable (R Studio 2012; Magnusson et al. 2017). Fixed effects included seeding method, species-specific seeding rate, interaction between method and seeding rate, site, and date sown. We also included a nested random effect for strip within block within array to account for the non-independence of the five quadrats per strip. Post hoc comparisons between seeding methods were conducted using Tukey's honest significant difference (HSD) test via the emmeans package (Lenth 2018). To assess average seeding rate effects on seeded species abundance for different seeding methods, we refit glmm models without the effects of site and date sown.

To determine whether first-year abundance metrics were a good indicator of longer-term abundance, we calculated the Pearson correlation between first-year and third-year abundances in seeded quadrats.

RESULTS

Which Seeding Method was Most Effective?

There were few consistent differences between seeding methods, despite substantial differences between arrays (Table 1; Figure 1). *Festuca* abundance did not differ between methods, while *Potentilla* density was higher in hydroseeded than drilled plots in year one and higher in both broadcast and hydroseeded than drilled plots in year three. For *Eriophyllum*, there were no differences between methods in year one, but cover was higher in broadcast than drilled plots in year three.

What is the Plant Establishment Response Based on Seeding Rate across Seeding Methods, Sites, and Seeding Dates?

Average plant abundance increased with seeding rate for each sown species in year one, and this effect persisted through year three (Figure 2; Table 1). Effects of site and of seeding date were weaker than the effects of seeding rate.

First-year establishment averaged approximately 4% for *Festuca*. Plant density was strongly affected by seeding rate in both year one and year three (Figure 2; Table 1). In year three, the relationship between abundance and seeding rate was stronger where seeds were broadcast or hydroseeded than where they were drilled. Establishment also varied strongly among sites, though not consistently over time: densities were higher at Glacial Heritage than the other sites in year one but lower at Tenalquot than the other sites in year three. Seeding date affected establishment in year one but not in year three.

First-year establishment averaged approximately 2% for *Potentilla*. Plant density was strongly affected by seeding rate in year one and year three (Figure 2; Table 1). Unlike the pattern for *Festuca*, seeding method affected establishment of *Potentilla* in year one but not in year three. In year one, plant abundance increased with seeding rate for broadcast and hydroseeded plots but not for drilled plots. Establishment varied strongly among sites; densities were highest at Tenalquot in both years one and three and were lowest at Scatter Creek in year one but did not differ between Scatter Creek and Glacial in year three.

First-year establishment averaged approximately 10% for *Eriophyllum*. Plant density in year one was strongly related to seeding rate, as was plant cover in year three (Figure 2; Table 1). Seeding rate and seeding method did not interact in either

Table 1. Summary of variable importance in models of plant density or cover. The values reported for each term are the chi-square statistic and *P* value from a likelihood ratio test comparing models with and without the term. *P* values <0.05 are bolded.

Species	Year	Date sown		Site		Method		Seeds		Method:Seeds	
		χ^2	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*
Eriophyllum	1	6.1	**0.013**	5.8	0.056	1.4	0.497	128.9	**<0.001**	1	0.599
	3	8.9	**0.003**	6.6	**0.038**	6.4	**0.041**	70.1	**<0.001**	1.4	0.509
Festuca	1	4.5	**0.035**	12.9	**0.002**	2.9	0.234	148.7	**<0.001**	3.9	0.142
	3	1.4	0.238	9	**0.011**	0.5	0.789	95.5	**<0.001**	10.4	**0.006**
Potentilla	1	-	-	20.4	**<0.001**	9	**0.011**	59.3	**<0.001**	10.2	**0.006**
	3	-	-	11.1	**0.004**	18.1	**<0.001**	46.6	**<0.001**	3.4	0.181

year. Abundance differed more strongly between seeding dates than among sites. Plant densities were higher at Glacial than Scatter Creek in year one, but plant cover was higher at Tenalquot than Glacial in year three.

Are First-Year Metrics Good Indicators of Future Abundance?

Abundances of individual plants in the first year of monitoring were positively correlated with abundances in the third year for all sown species (Figure 3). The strength of this correlation varied among species and sites. Correlations were strongest at Tenalquot and were weakest at Glacial Heritage for *Eriophyllum* and *Potentilla* and at Scatter Creek for *Festuca*.

DISCUSSION

Availability of appropriately sourced native seed is often one of the primary limiting factors in the restoration process (Rowe 2010) and it is vital that seeding methods, rates, and timing are appropriate for the environment in which they are used. Our results provide insights into when and under what ecological conditions certain seeding techniques may be effective. Refined seeding methods, along with appropriately scaled (over time and space) monitoring of restoration sites, can guide adaptive management and help develop clear ecological goals (Rinella et al. 2012).

Seeding Method

Seeding method affected the establishment of both forbs in our seed mix, with drilling resulting in lower abundance than the other methods by year three. Seeding method did not affect establishment of *Festuca*, though it did have a long-term interactive effect with seeding rate. Seed drilling is generally favored for graminoids in rangeland and dry grassland systems where desiccation and overexposure to ultraviolet light can negatively impact establishment (Doerr et al. 1983; Thompson et al. 2006; Mollard and Naeth 2014). However, seeds sown in the rainy season of Pacific Northwest prairies are unlikely to experience these issues. Furthermore, the need for specialized seed drilling equipment makes it more costly to establish plants using this method. We do not recommend drilling in this ecosystem.

Brown and Rice (2001) found simulated hydroseeding to be an inferior method of establishing native grasses in California. After three years of monitoring, differences between hydroseeded and broadcast plots were relatively minor in our study. However, the costs and expertise necessary to carry out simulated hydroseeding are much higher than those for broadcasting. We recommend broadcasting as the most effective and cost-efficient seeding method of the three that we evaluated.

Seeding Rate

As expected, higher seeding rates resulted in higher plant densities. However, establishment remained low: the average density of any sown species never topped 10% of the amount of sown seed and was often less than 5%. Other native seeding efforts have found fairly low establishment rates (<17%), with the highest bottleneck occurring between germination and establishment phases (Clark et al. 2007; James et al. 2011). Low establishment rates are fairly typical for the species used in this study; a laboratory study under optimal stratification treatment conditions found a maximum germination rate of 31% for *Eriophyllum* and 21% for *Potentilla* (Drake et al. 1998). All of our seeding rates were calculated in terms of bulk seed (i.e., not accounting for seed viability or additional chaff), as pure live seed (PLS) data were not available for the seed lots used in this experiment. Because of this, our reported establishment rates are lower than they would be if we had seeded using rates based on PLS. More recent (2014) seed lots of *Festuca*, *Potentilla*, and *Eriophyllum* had PLS estimates of 35%, 73%, and 51%, respectively. Furthermore, different seed lots were used for the two different seeding dates, to limit loss of viability over a year in storage. This could have contributed to variability in establishment between seeding dates (Gallagher and Wagenius 2016). As the restoration community strives to apply agricultural techniques to sowing, it should also start applying agricultural techniques to seed production and incorpo-

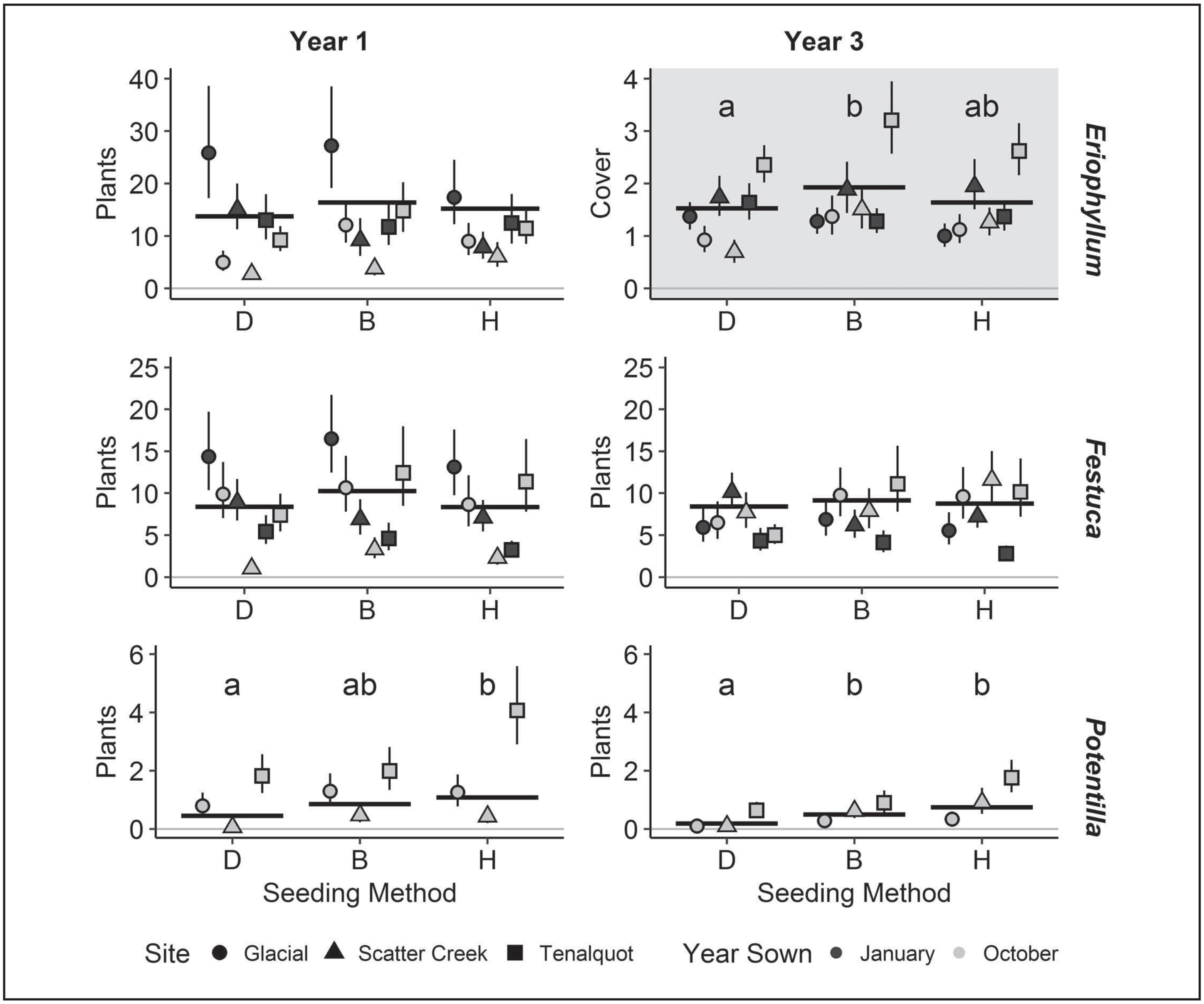

Figure 1. Mean abundances (± 95% confidence intervals) of each species in each site (symbol shape) and seeding date (color) when monitored one year and three years after seeding. Significant differences (α = 0.05) between seeding methods (D = Drill, B = Broadcast, H = Hydroseed) are shown by different letters. Panels without letters had no significant differences between treatments. The grand mean for each seeding method across sites and seeding dates is shown by a thick horizontal line. The gray panel indicates where abundance was measured as percent cover; in all other panels, abundance was measured as density (plants/m^2). Statistical results are in Table 1.

rating PLS information when determining seeding rates. We did not detect evidence of a threshold above which establishment decreased, suggesting that even at the highest rates tested these species remain seed limited. Thus, the maximum seeding rates used here would be expected to positively influence establishment in other settings. Further research is required to assess the establishment responses to even higher seed densities, and to identify appropriate rates when establishing diverse plant communities.

The appropriate sowing rate must also take into consideration a suite of abiotic (light and water availability, soil contact) and biotic (seed predators, pathogens, competitors) factors that could limit establishment (Clark et al. 2007). Seed predation and seedling herbivory may have led to low field establishment rates in this study. Previous work in western Oregon found that 21% of *Bromus carinatus* Hook. and Arn. seed was lost to vertebrate predation (Clark and Wilson 2003). In burned prairies, as much as 55% of seed can be removed by predators (Reed et al. 2004). While burning our sites prior to sowing was necessary to create space for seed–soil contact, litter removal makes seeds more accessible to rodents (Reed et al. 2004, 2006). Alternatively, burning removes the safe cover for surface-dwelling small mammals, limiting their access and activity for several months post-burn (Clark and Kaufman 1990). The

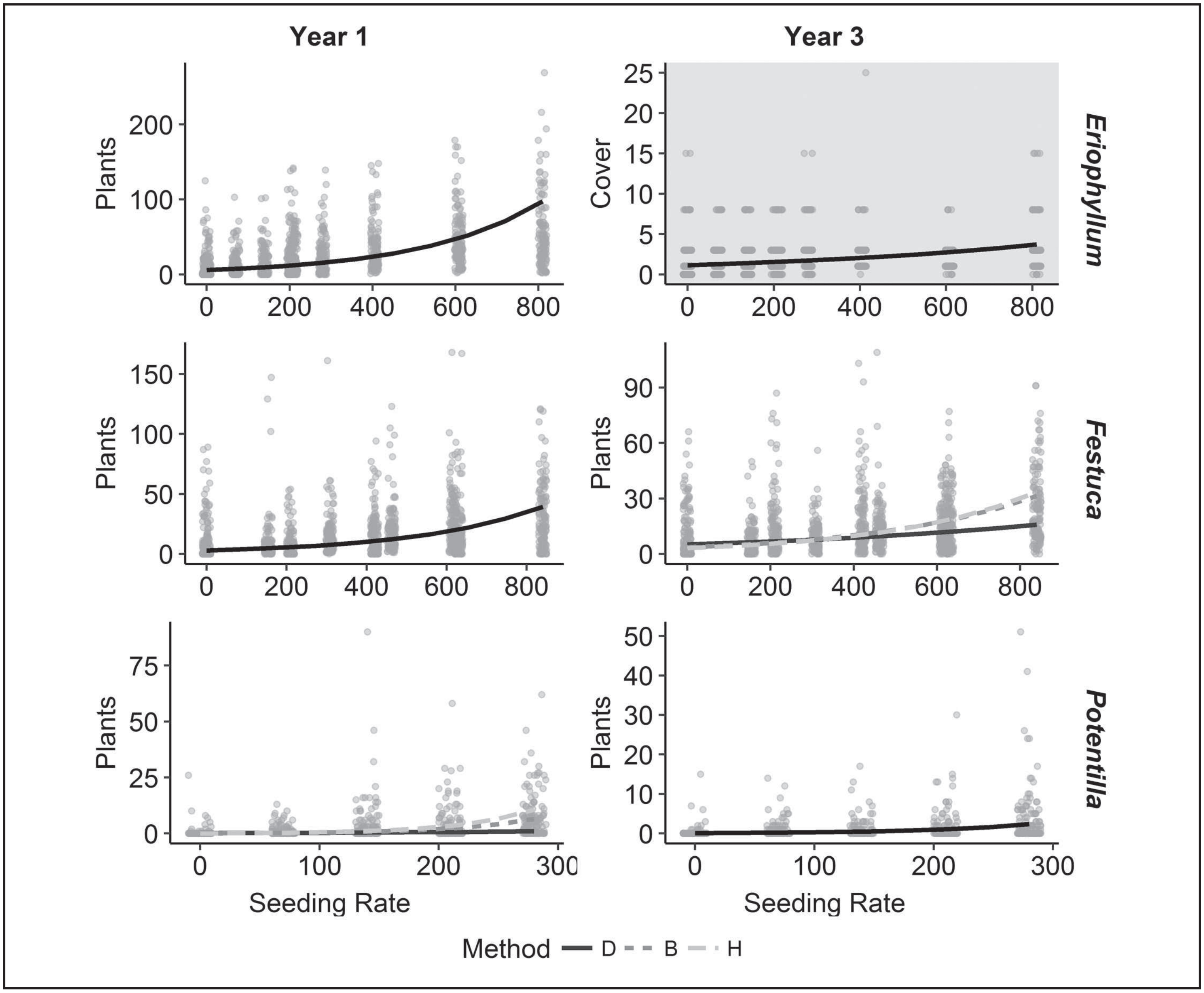

Figure 2. Relationship between seeding rate (seeds/m^2) and abundance of *Eriophyllum lanatum, Festuca roemeri*, and *Potentilla gracilis* when monitored one year and three years after seeding. Panels with a single black curve had a significant effect of seeding rate but no interaction between rate and seeding method; lines of differing color and pattern are shown where the interaction was statistically significant. The gray panel indicates where abundance was measured as percent cover; in all other panels, abundance was measured as density (plants/m^2). Statistical results are in Table 1.

impact of seed predation on establishment likely varies by species and site (Whelan et al. 1990); more information on the identity and seasonal activity of seed predators and herbivores would provide options for protecting seeds and seedlings against predation and herbivory.

Consistency of Treatment Effects

Sites exhibited strikingly high variation in overall establishment rates even though they are geographically close to one another and the plot locations had similar plant communities. For example, Scatter Creek is only a few kilometers away from Glacial Heritage, yet often had lower abundances of sown species. Although these sites were seeded at the same time and with the same seed lot, these differences in establishment are likely a reflection of differences in the biotic and abiotic factors such as soil nutrient and water availability, mycorrhizal associates, or herbivory. While the plant species richness (approximately 55 native species and 30 nonnative species) and community composition were similar between sites, the abundance of certain invasive species within each treatment area may have differed. A 2008 survey showed that Scatter Creek had greater invasion of Scotch broom and tall oatgrass (*Arrenatherum elatius* [L.] P. Beauv. ex J. Presl and C. Presl) than Glacial Heritage (Washington Department of Fish and Wildlife, unpub. data), and both of these species can affect the soil suitability for native species (Haubensak and Parker 2004; Patra et al. 2006). Considering these

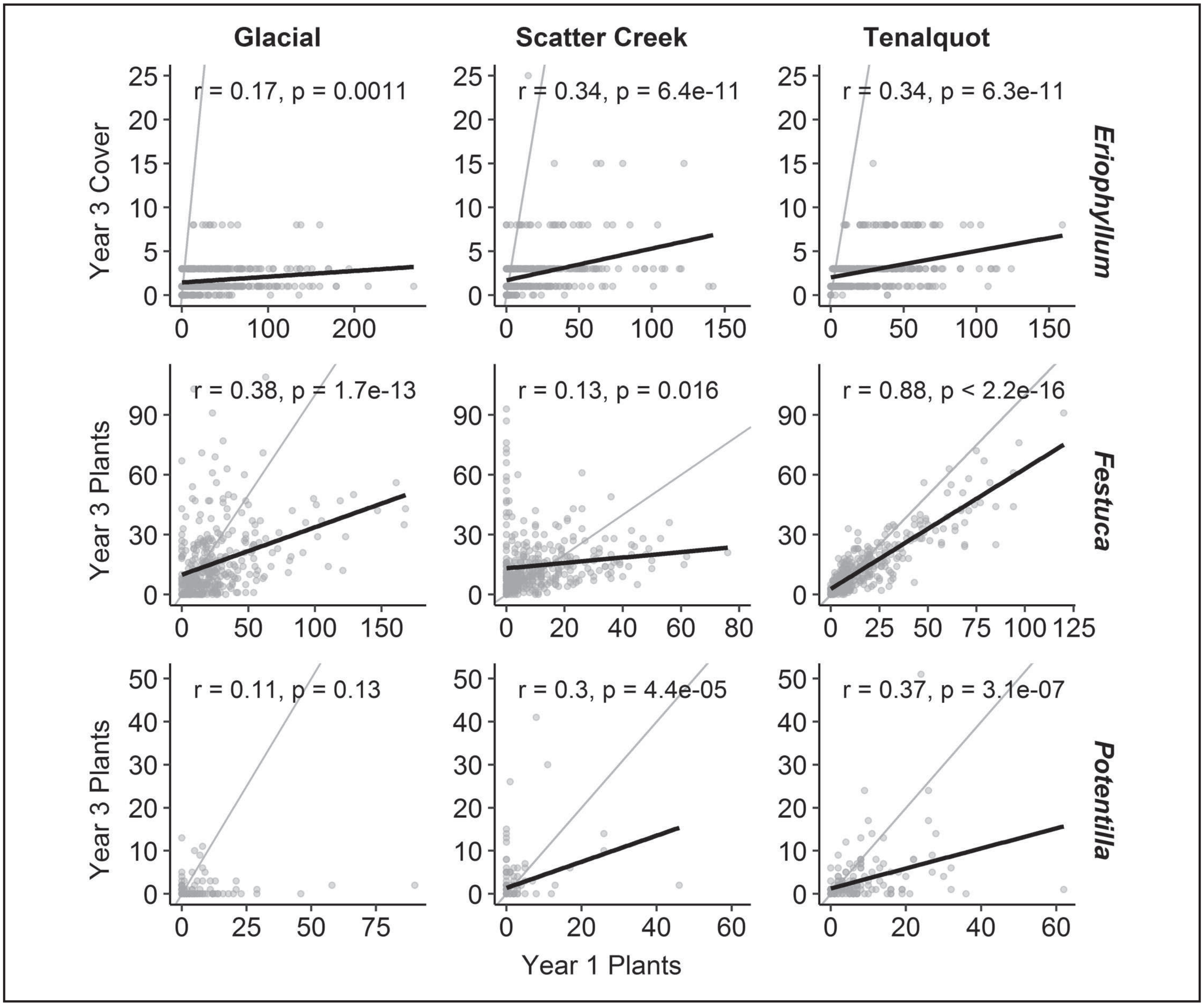

Figure 3. Correlations between first- and third-year abundances of *Eriophyllum lanatum, Festuca roemeri,* and *Potentilla gracilis* at each site. Data points are seeded quadrats (quadrats that received no seed were excluded). Fit lines are shown in black where statistically significant (α = 0.05), and the 1:1 relationship is in gray. Abundance was measured as density (plants/m^2) in all cases except for the Year 3 response for *Eriophyllum*, which was in percent cover.

potential impacts, it may be important to use an adaptive approach and tailor seeding rates and methods to individual sites (Bakker et al. 2018).

Weather and microsite conditions presumably influenced overall establishment differences between seeding dates. In particular, the weather was much cooler following the October seeding than the January seeding. Between seeding and monitoring the following spring, there were nearly three times more days with freezing temperatures after the October seeding (PRISM Climate Group 2015). The cold–moist stratification needs of each of the tested species were presumably met by both sowing times, due to the short to moderate stratification times needed (0–3 wk for *Festuca roemeri*, 4–6 wk for *Potentilla gracilis*, 9–12 wk for *Eriophyllum lanatum*; Kuykendall 2002; Skinner 2007, 2008). The influence of the forest edge in the October-sown arrays at Scatter Creek and Glacial Heritage may have contributed to the poorer overall establishment due to additional shading, subsequent lower temperatures, and competition from nonnative species (as opposed to Tenalquot, where January and October arrays were similarly shaded).

Long-Term Success

Sown plant densities generally declined over time. As a result, seeding rate was only moderately correlated with third-year abundance, though first-year abundance was a strong indicator of third-year abundance. Given that grassland plant communities change continually (Carter and Blair 2011), it is important that we continue to monitor restoration actions rather than assuming, as is commonly done, that a single assessment of establishment soon after seeding is sufficient to claim restoration success. This agrees with other grassland research showing that short-term results are not always predictive of long-term performance (up to 15 y post-seeding) for seeded grassland species (Rinella et al. 2012). Additionally, the strength of the correlation between first- and third-year abundances differed strongly among sites in this study, indicating that conclusions about long-term patterns require verification at individual sites.

CONCLUSIONS

In these mesic prairies, broadcast and simulated hydroseeding did not produce significantly different outcomes, suggesting that the extra effort and money required to add hydromulch is not necessary. Additionally, broadcast seeding resulted in more consistent and reliable establishment of native prairie plants than seed drilling. Species were seed limited even at the highest seeding rates. First-year metrics were positively correlated to third-year metrics, but the strength of this correlation varied greatly by site and species. Due to variability in establishment, restoration projects should monitor results for several years after sowing to assess whether long-term goals are being met.

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