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RESEARCH ARTICLE

Improving dryland seedling recruitment using fungicide seed coatings

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Abstract

1. The success of seed-based restoration in dryland regions of the world is often low or sporadic, with most mortality occurring between germination and emergence. Fungal pathogenesis is one process that may reduce seedling emergence and limit restoration success.
2. Our objective was to determine whether fungicide seed coatings constitute an economically viable strategy for increasing emergence by reducing fungal pathogenesis and mortality.
3. We performed an experiment across two sites and three years, using bluebunch wheatgrass (*Pseudoroegneria spicata*) as a model species. We found that fungicide coatings increased germination by 8.8% and emergence by 54.0% on average compared to the control. A cost analysis indicated that the fungicide coating was economically viable with an average estimated effective cost reduction of 18.8% under the study conditions.
4. There was a strong interaction ($P < 0.001$) between the effects of the fungicide coating, site and year on emergence. The fungicide coating increased emergence compared to the control in five of the six sites and years, with the effect ranging from a 33.7% decrease ($P = 0.042$) to a 150.9% increase ($P = 0.004$).
5. The observed interaction was likely related to the effect of the hydrothermal microsite environment on disease severity. In the site and year that the fungicide coating performed worse than the control, prolonged periods of exceptionally low soil moisture may have reduced disease severity through a variety of individual and community scale mechanisms.
6. Overall, these results indicate that fungicide seed coatings have the potential to improve dryland restoration efforts.

KEYWORDS
cost analysis, germination, hydrothermal microsite, rangeland management, restoration, seed enhancement technology, seed pathology, seedling emergence

1 | INTRODUCTION

Direct seeding is often utilized in ecological restoration to re-establish native plant communities following disturbance or weed invasion (Erickson et al., 2017; Leger et al., 2019; Shackelford et al., 2021). Biotic and abiotic stressors commonly inhibit seeding efforts in dryland regions of the world (Aradottir & Hagen, 2013; Svejcar et al., 2017), which frequently results in low or sporadic success, despite large expenditures (Bodin et al., 2021; Kildisheva et al., 2016; Kimball et al., 2015; Knutson et al., 2014; Shackelford et al., 2021). For many species, most of the mortality that contributes to seeding failure occurs during the critical demographic period between germination and emergence (Hardegree et al., 2020; James et al., 2011, 2019). Thus, treatments and practices that address the biotic and abiotic processes limiting survival during this demographic stage will have the greatest potential to increase the likelihood of restoration success (Copeland et al., 2021).

Pathogenesis is one process that may limit survival of seeds and seedlings. The highest rates of disease-related mortality of plants in natural systems commonly occur during these demographic stages (Blaney & Kotanen, 2001; Gilbert, 2002; Mackin et al., 2021). Fungi and oomycetes (henceforth referred to collectively as fungi) are particularly important contributors to seed decay and seedling disease (Fawke et al., 2015; Gilbert, 2002). Fungal pathogens may encounter and colonize seeds and seedlings via seed-borne or soil-borne pathways. Each pathway can simultaneously support a diversity of fungal pathogens that may interact to contribute to decay, disease and mortality through a variety of mechanisms (Baskin & Baskin, 2014; Chambers & MacMahon, 1994; Mackin et al., 2021; Nelson, 2018). Given the diversity of fungal pathogens on seeds and in soils, the potential for fungal pathogenesis as a limiting process to plant establishment in a restoration context is high (Franke et al., 2014; Lamichhane & Venturi, 2015; Nelson, 2018).

Fungal pathogenesis of seeds and seedlings is promoted by long incubation periods associated with seed dormancy under cool, moist conditions (Dalling et al., 2011; Gornish et al., 2015; Nelson, 2018; Kildisheva et al., 2020). Because seed dormancy is prevalent in over 80% of dryland species, fall dormant seedings are typical of dryland restoration projects (Baskin & Baskin, 2014). Seeding in the fall allows seeds to reach the hydrothermal accumulation thresholds required to overcome their dormancy, thereby priming them for emergence when conditions are favourable for plant growth in the spring (Beyers, 2004; Hardegree et al., 2018; James et al., 2019). In temperate drylands, the winter incubation period is conducive to fungal activity and growth due to the wet, cool conditions associated with snow cover (Aanderud et al., 2013; Gornish et al., 2015; Kuhnert et al., 2012). Therefore, fall-seeded, dormant seeds may be exposed to high pathogen loads for 4–5 months before emerging in the spring.

The relationship between dormant seeds and pathogens has been described as a race for survival (Beckstead et al., 2007). In this scenario, seeds and pathogens are in direct competition for endosperm resources, each seeking to utilize the resources before the other. Microsite environmental factors such as soil moisture and temperature may give a competitive advantage to either the seed or the pathogen (Allen et al., 2018; Mackin et al., 2021). Fungal pathogenesis can also be exacerbated by abiotic stressors such as freeze–thaw cycles or drought conditions (Allen et al., 2018; Connolly & Orrock, 2015). Thus, disease severity can be highly dependent on the weather. As weather variability increases due to climate change, fungal seed decay and seedling disease may have an increasingly important effect on the population dynamics of host species and restoration efforts (Allen et al., 2018; Connolly & Orrock, 2015; Gilbert, 2002).

Limitations to seeding success associated with fungal seed decay and seedling disease can be addressed using fungicide seed coatings. Fungicide seed coatings may address ectophytic seed- and soil-borne diseases systemically or by creating a 'protective zone' surrounding the seed depending on the translocation of the fungicide (Nuyttens et al., 2013). While fungicide seed coatings are commonly used in agriculture to reduce seedling mortality and improve yield, the application of fungicides in restoration scenarios has been limited (Krupinsky et al., 2002; Munkvold, 2009; Nuyttens et al., 2013; Pedrini et al., 2020). Furthermore, seed enhancement technologies have only recently been adapted to ecological restoration (Madsen et al., 2016; Pedrini et al., 2017; Pedrini et al., 2020). In agriculture, fungicides are commonly applied to seeds using a film coating (Accinelli et al., 2018; Pedrini et al., 2018; Pedrini et al., 2020). The process for film coating seeds includes mixing seeds in a rotating drum while adhesives (or binders) and liquid treatments such as fertilizers, protectants or surfactants are pumped onto a spinning disk (Madsen et al., 2016; Pedrini et al., 2017; Accinelli et al., 2018; Pedrini et al., 2020). This method uniformly distributes the treatment directly onto the seed. Due to the targeted nature of seed coatings, relatively small amounts of fungicide are required to produce a treatment effect, which reduces the potential of exposure of active substances to non-target organisms and increases the economic efficiency of the treatment (Munkvold, 2009; Nuyttens, et al., 2013).

The purpose of this study was to determine whether seed and seedling mortality due to fungal pathogenesis in dryland restoration seedings can be mitigated by applying a fungicide seed coating. To accomplish this, we used bluebunch wheatgrass (*Pseudoroegneria spicata*), a dominant, native bunchgrass in the Intermountain West, USA, as a model species. Bluebunch wheatgrass represents an ideal model species because it is one of the most common native grasses seeded in the Intermountain West, it is well-studied, and the fungal pathogens associated with its seeds have been documented (Gornish et al., 2015). This allowed us to choose fungicides that target fungal pathogens known to be associated with bluebunch wheatgrass seeds. These include *Fusarium tricinctaum*, *Fusarium solani*, *Sclerotinia homoeocarpa*, *Fusarium fujikuroi*, *Verticillium dahlia* and *Davidiella tassiana* (Gornish et al., 2015). Bluebunch wheatgrass is typically seeded in the fall and is likely to be exposed to fungal pathogenesis as it is incubated in the soil over the winter in a cool, wet environment.

Our objectives were to (1) evaluate whether fungicide seed coatings affect bluebunch wheatgrass germination and growth under controlled conditions with limited pathogenic pressure, and (2) determine in situ whether fungicide seed coatings constitute an economically viable treatment to improve dryland seeding success. We hypothesized

TABLE 1 The characteristics of the fungicides applied to bluebunch wheatgrass via seed coating and the corresponding active ingredients

Fungicide trade name	Active ingredient	Pathogens addressed	Half-life (days)	Applied rate ($mg_{fungicide}/g_{seed}$)	Applied rate ($g_{a.i.}$/ha)
Apron XL®	Mefenoxam	Oomycetes (e.g. *Pythium*)	70	0.775	2.388
Maxim 4FS®	Fludioxonil	Broad spectrum (e.g. *Fusarium*, *Verticillium*)	69	0.207	0.747
Dynasty®	Azoxystrobin	Broad spectrum (e.g. *Pythium*, *Fusarium*)	14	1.195	1.029
Thesis®	Difenoconazole	Broad spectrum (e.g. *Fusarium*, *Verticillium*)	120	0.427	0.296

Note: The applied rates are 167% of the labelled rates for similar agricultural species. The half-lives represent averages under field conditions. The applied rates ha^{-1} assume a seeding rate of 9.0 kg PLS ha^{-1}.

that the fungicide seed coating would cost-effectively increase germination and seedling emergence under field conditions.

2 | MATERIALS AND METHODS

2.1 | Laboratory trial

Research was performed using 'Anatone' bluebunch wheatgrass purchased from Granite Seed and Erosion Control (Lehi, UT, USA). Seeds were coated with four fungicide products that address the pathogens identified by Gornish et al. (2015), as well as oomycete pathogens. The trade names for these products are Apron®, Dynasty®, Maxim® and Thesis® (Syngenta, Basel, Switzerland), and the active ingredients are mefenoxam, azoxystrobin, fludioxonil and difenoconazole, respectively (Table 1). Mefenoxam is a xylem-mobile fungicide that interferes with DNA and RNA synthesis of oomycetes. Fludioxonil is a contact fungicide that disrupts signal transduction. Azoxystrobin and difenoconazole are systemic fungicides that inhibit respiration and fungal cell wall synthesis, respectively.

Whereas most agricultural species typically emerge from the soil a few days to weeks after seeding, dryland seeds sown in the fall remain in the soil for several months and consequently may be subject to pathogenic pressure for a longer period than their agricultural counterparts (Nelson, 2018). For this reason, and in the absence of recommended rates for dryland applications, we chose to apply rates that were approximately 67% higher than the labelled rates designated for forage grasses or wheat. These rates remained well below the maximum allowable application rates on an active ingredient per unit area basis, assuming a seeding rate of 9.0 kg PLS ha^{-1} (Table 1).

We coated bluebunch wheatgrass seed with the fungicides using a 31-cm diameter rotary drum seed coater (Universal Coating Systems, Independence, OR, USA). We used Agrimer SCP I (Ashland Inc., Covington, KY, USA) as a binder and limestone powder ($CaCO_3$) as a filler material. Seed coating was performed on 200 g of seed, with the drum rotating at 20% of its maximum velocity. Seeds were first coated with 20 ml of a dilution composed of the four fungicides and binder (Table 1). Directly following the application of the fungicide–binder mixture, we gradually added small amounts of limestone and binder in alternating steps, using standard seed coating techniques (Pedrini et al., 2020), until a total of 350 g of limestone powder and 128 ml of binder were applied. During the coating process, the limestone powder was delivered directly over the seed, and the binder and fungicide were applied to the spinning disk using a syringe. This technique encrusted the seed in a durable layer, maintaining the treatment in close proximity to the seed. The seed was then dried using a forced-air dryer (Braceworks Automation and Electric, Lloydminster, SK, Canada) at 43°C for approximately 7 min.

In addition to the fungicide seed coating described above, our study included a treatment composed of seeds coated with only binder and limestone powder (blank). The blank coating served as a procedural control to observe the effects of the coating alone without the effects of the fungicide. We also included a treatment with the seeds left uncoated (control). We tested seed germination and plant growth on these seed treatments in separate studies. For each study, we placed 10 replicate samples of 25 seeds of each treatment on fine sand within 11.0 cm × 11.0 cm × 3.5 cm covered acrylic containers. All containers were watered to field capacity and placed in Precision Plant Growth Chambers (Thermo Fischer Scientific, Waltham, MA, USA) at 15°C with 12 h light/dark cycles. Both studies were organized using a randomized complete block design using blocks to account for positional variability within the incubator. The positions of the blocks and containers within blocks were rearranged twice a week throughout the studies.

For the germination study, we recorded the number of seeds with a radicle exceeding 2 mm in length every 2–4 days for 31 days. Seeds that had germinated were removed from the container at the time of counting. From the germination data, we estimated the time to reach 50% germination (T_{50}), and final germination percentage (FGP) using nonlinear, three-parameter log-logistic time-to-event models (Ritz et al., 2013). Time-to-event models were fit using the 'drm' function of the 'drc' package (Ritz et al., 2015) in the R programming environment (R Core Team, 2020). We performed pairwise comparisons between treatments using the 'compParm' function in the 'drc' package and adjusted the *P*-values using the Bonferroni method for comparing a family of three estimates ($\alpha = 0.05$).

In the biomass study, plants were allowed to grow for 31 days and then harvested. Plants were harvested by washing the sand from the roots and then drying them at 105°C for 3 days. After drying, root biomass and shoot biomass were measured separately. We analysed total biomass and the root-to-shoot ratio using linear mixed-effects models, with blocks included as a random effect (Bates et al., 2015). Linear mixed-effects models were fit using the 'lmer' function of the 'lme4' package in the R programming environment (Bates et al., 2015; R Core Team, 2020). We performed pairwise comparisons between

treatments using the 'emmeans' function of the 'emmeans' package in the R programming environment (Lenth, 2021; R Core Team, 2020) and adjusted the *P*-values using the Bonferroni method for comparing a family of three estimates ($\alpha = 0.05$).

2.2 | Field trial

We conducted experiments to determine the effects of the fungicide coating on germination and emergence under field conditions at two sites near Lookout Pass (40.139003, −112.507367) and Santaquin (39.907287, −111.816306), Utah, USA. Further description of the sites, including climate, soil characteristics and site preparations, can be found in Appendix S1. Permission to use the research sites for experimental purposes was granted by the corresponding government agencies.

Soil moisture and temperature were measured in a central location at each site using two MPS-6 water potential sensors (METER, Pullman, WA) that were buried 2 cm below the soil surface. Daily average soil temperature and water potential were calculated to compare the soil hydrothermal environment between sites. Long-term and monthly averages of precipitation and ambient temperatures were also derived from models produced by PRISM's (Parameter-elevation Regressions on Independent Slopes Model) Oregon Climate Service (PRISM Climate Group, 2020). The long-term averages were taken from 1981 to 2010.

We organized the field germination and emergence experiment following a randomized complete block split-plot design with sites and years comprising the whole plots and blocks comprising the subplots. Blocks contained three seed treatments, control, blank and fungicide-coated seed, sown in separate rows spaced approximately 50 cm apart, with seeds sown about 1 cm deep. The study was implemented over three years, from 2016 to 2018, with seeding occurring each year between October 20 and November 3. We modified some aspects of the study design following the 2016 seeding season due to the preliminary nature of that portion of the study (Table 2). In 2016, seeds were sown in 3 m rows, whereas in 2017 and 2018, seeds were sown in 1.5 m rows within 15 cm deep furrows (Table 2). The same seed variety and species used in the laboratory trial was used in the field, with separate seed lots purchased from Granite Seed and Erosion Control in each seeding year.

TABLE 2 Approximate sample sizes per treatment by year

	Sample size per treatment	
Year	Germination	Emergence
2016	250	5340
2017	800	2800
2018	800	2620

Note: For the germination experiment, the sample size varied according to the number of germination bags (five per treatment and site in 2016 and 10 in 2017–2018) and the number of seeds per germination bag (25 in 2016 and 40 in 2017–2018). For the emergence experiment, the sample size varied according to the length of the rows (3 m in 2016 and 1.5 m in 2017–2018) and the labelled viability of the seed. For the germination experiment, we note that slight variations from the intended sample sizes occurred due to human errors (see Hoose et al., 2022). For the emergence experiment, we assumed that seeds were sown at the intended seeding rate of 82 PLS m^{-1}.

In 2016, seeds were coated following the same procedure as the laboratory study. However, in 2017 and 2018, we replaced Thesis® in the fungicide coating with Dividend® because Thesis® was discontinued. Like Thesis®, the primary active ingredient of Dividend® is difenoconazole, but Dividend® also contains a small amount of mefenoxam. We also modified the binder used from Agrimer SCP I in 2016, to Agrimer SCP II (Ashland Inc., Covington, KY, USA) in 2017 and 2018, which improved the stability of the coating.

To evaluate germination response to the treatments, we planted mesh bags (SumDirect ®, Dongguan Fuxin Electronics Co Ltd, Henglitown, Guangdong, China), henceforth germination bags, that each contained seeds of a single treatment and sieved soil that was collected from the site in which the bag was planted (Abbott & Roundy, 2003). In 2016, we buried germination bags in individual rows in five blocks, while in 2017 and 2018, we buried germination bags in individual rows in 10 blocks (Table 2). In 2016, each germination bag contained approximately 25 seeds, while in 2017 and 2018, each germination bag contained approximately 40 seeds (Table 2). Germination bags were harvested each year in March. In the laboratory, we separated the seeds from the soil by lightly washing the contents of the bag over a fine mesh screen. Seeds were considered germinated when the radicle exceeded 2 mm. We evaluated the emergence treatment response by sowing seeds of each treatment in rows organized in 10 blocks at an approximate rate of 82 PLS m^{-1}. We counted emergence in April of each year.

We evaluated the effect of fungicide seed coatings on the proportion of germinated and emerged seedlings using generalized linear mixed-effects models with a binomial response distribution (Sileshi, 2012; Bates et al., 2015). Following this modelling structure, individual seeds comprised the experimental units. Because seeds were grouped in germination bags for germination tests and rows for emergence tests, germination bags and rows were included in the models as random effects. Block and year were also defined as random effects with germination bags and rows implicitly nested within blocks, and blocks implicitly nested within sites and years. Treatments and sites were defined as fixed effects. Germination and emergence models were fit using the 'glmer' function of the 'lme4' package in the R programming environment (Bates et al., 2015; R Core Team, 2020).

The significance of all two- and three-way interactions between treatment, site and year was tested by comparing models with and without individual interaction terms using likelihood ratio tests. Due to significant interactions, we also fit separate models for each year and site. We performed pairwise comparisons between treatments using the 'emmeans' function of the 'emmeans' package in the R programming environment (Lenth, 2021; R Core Team, 2020) and adjusted the *P*-values using the Tukey method for comparing a family of three estimates ($\alpha = 0.05$).

TABLE 3 Itemized summary of the estimated costs of producing fungicide-coated seed for researchers and commercial applications

	Seed coating costs ($/kg$_{seed}$)	
Item	Research	Commercial
Apron XL®	$0.77	$0.42
Maxim FS®	$0.20	$0.11
Thesis®	$1.19	$0.60
Dynasty®	$0.42	$0.24
Binder	$3.79	$0.55
Ca. carbonate	$0.11	$0.11
Operational costs	$0.77	$0.77
Total cost	$7.28	$2.80

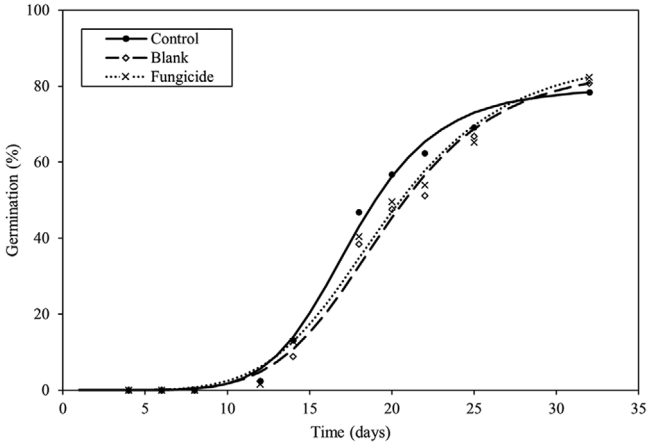

FIGURE 1 Cumulative germination percentage across time for the control, blank and fungicide treatments in the laboratory experiment. Points represent average cumulative germination percentage on each count date and lines represent fitted time-to-event model curves

2.3 | Cost analysis

The economic viability of a seed treatment can be assessed by dividing the treatment cost by a measure of success (Boyd & Davies, 2012; Kimball et al., 2015; Pedrini et al., 2020). If a seed treatment improves the probability of success more than it increases the cost, compared to a control, then the treatment is economically viable. In this study, we used emergence as a measure of success. Thus, we tested the economic viability of fungicide seed coatings by dividing the estimated costs of control and fungicide-coated seed by the respective estimated probabilities of emergence (Kimball et al., 2015; Pedrini et al., 2020). We estimated the cost of bluebunch wheatgrass based on personal communications with the Utah Division of Wildlife Resources Great Basin Research Center and Seed Warehouse (Ephraim, UT, USA). We estimated the cost of fungicide coatings by adding the estimated costs of materials and seed coating operation at the industrial scale (Table 3). These values reflect personal communications with Syngenta and Summitt Seed Coatings (Caldwell, ID, USA). We divided the cost of the control and fungicide-coated seed by their respective average emergence percentages, weighted equally by year (Kimball et al., 2015). We also tested the economic viability of the fungicide treatment across a range of seed costs, treatment costs and treatment effects to improve generalizability.

3 | RESULTS

3.1 | Laboratory trials

The FGP estimates of the control, blank and fungicide treatments were 79.8% ± 2.7%, 85.6% ± 3.0% and 88.3% ± 3.1%, respectively, with no significant differences between them ($P > 0.050$; Figure 1; Table 4). Both the fungicide and the blank coatings slowed germination, with T_{50} estimates 1.93 ± 0.64 days ($P = 0.007$) and 1.99 ± 0.59 days ($P = 0.002$) greater than the control (17.59 ± 0.34 days), respectively (Figure 1; Table 4). The fungicide coating increased seedling biomass over the control by 40.7% ± 13.3% ($P = 0.020$) and the blank by 29.4% ± 12.2% ($P = 0.082$; Table 4). The root-to-shoot ratios of the control, blank and fungicide coatings were 1.27 ± 0.18, 1.37 ± 0.20 and 1.63 ± 0.25, respectively, with no significant differences between them ($P > 0.050$; Table 4).

3.2 | Field trials

Santaquin and Lookout Pass experienced higher than normal precipitation during the seed incubation period (i.e. October through April) in 2016 and 2018, but lower than normal precipitation in 2017 compared to long-term averages (Figure 2). At Lookout Pass, in 2017, soil conditions were exceptionally dry compared to other sites and years with only 21% of the incubation period characterized by water potentials above −1.3 MPa, the germination threshold for bluebunch wheatgrass (Hardegree et al., 2003; Figure 3). By contrast, more than 75% of the incubation period was characterized by soil water potentials above −1.3 MPa in the remaining sites and years (Figure 3). Soil water potential was also more variable at Lookout Pass in 2017 than in other sites and years (Figure 3). Temperatures at both sites were generally similar to the long-term averages, although both sites experienced slight warm spikes in January of 2018 (Figure 2). Soil moisture was generally considerably higher in Santaquin than Lookout Pass, but temperatures were fairly similar between sites (Figures 2 and 3).

Across all sites and years, the average germination percentages, weighting each year equally (Table 2), for the control, blank and fungicide treatments were 80.0%, 79.8% and 87.0%, respectively (Figure 3). We identified interactions between the year and the treatment ($P < 0.001$) and the year and the site ($P < 0.001$), which complicated meaningful interpretation of treatment effects across all sites and years. The fungicide coating increased germination compared to the control in three of the six (50.0%) sites and years with effects ranging from a 2.5% decrease in germination (Lookout Pass 2017;

TABLE 4 A summary of pairwise comparisons between treatments for each response in the laboratory trials

Response	Pairwise comparison	Difference	*SE*	*P*
Final germination percentage (%)	Control – Blank	−5.80	4.02	0.450
	Control – Fungicide	−8.50	4.11	0.114
	Blank – Fungicide	−2.73	4.32	0.999
Time to 50% germination (days)	Control – Blank	−1.99	0.593	0.002
	Control – Fungicide	−1.93	0.638	0.007
	Blank – Fungicide	0.062	0.722	0.999
Biomass (g)	Control – Blank	−0.004	0.007	0.999
	Control – Fungicide	−0.022	0.007	0.020
	Blank – Fungicide	−0.017	0.007	0.082
Root–shoot ratio	Control – Blank	−0.109	0.181	0.999
	Control – Fungicide	−0.365	0.181	0.176
	Blank – Fungicide	−0.256	0.181	0.520

Note: *P*-values were adjusted for multiple comparisons using the Bonferroni method for comparing a family of three estimates ($\alpha = 0.05$).

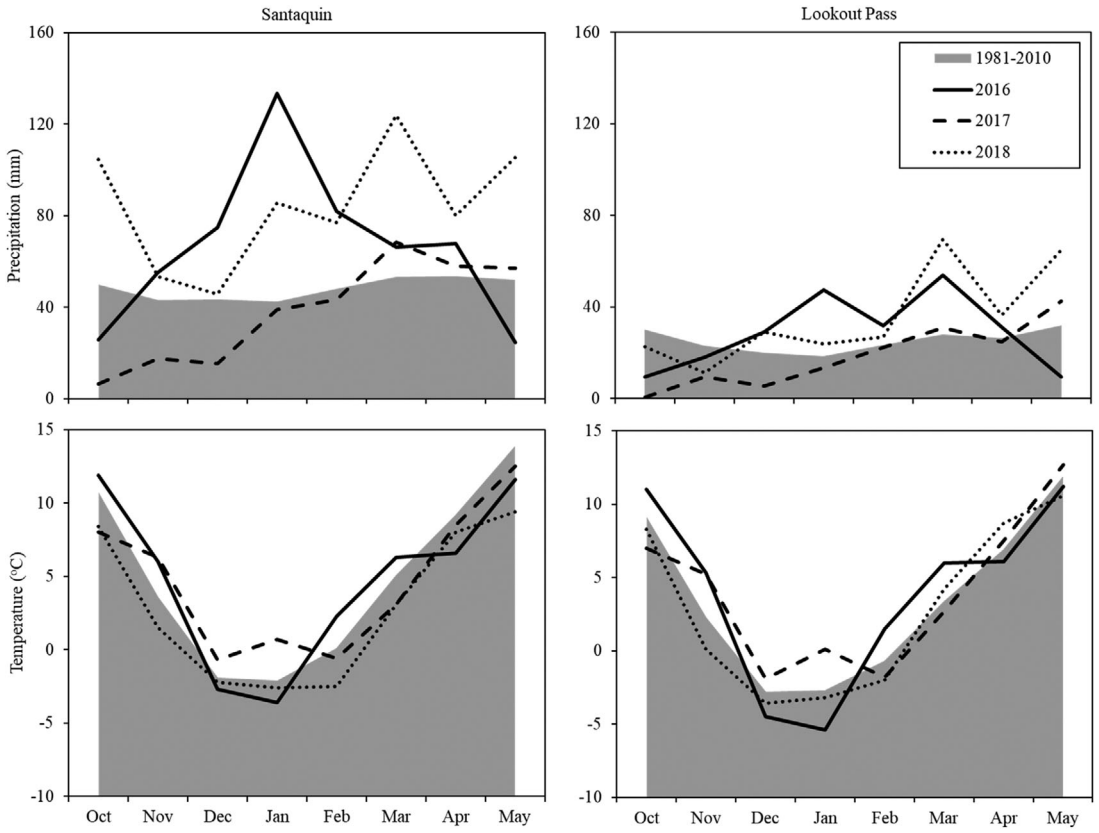

FIGURE 2 Monthly average precipitation and temperature between seeding and emergence at each site and year compared with the 30-year average

$P = 0.753$) to a 25.2% increase in germination (Lookout Pass 2018; $P < 0.001$; Figure 3). The blank performed similarly to the control in all sites and years (Figure 3).

Across all sites and years, the average emergence percentages, weighting each year equally (Table 2), for the control, blank and fungicide treatments were 17.5%, 18.1% and 26.9%, respectively. We identified a significant three-way interaction between the treatment, the site and the year ($P < 0.001$). The fungicide coating increased emergence compared to the control in five of the six (83.3%) sites and years with effects ranging from a 33.7% decrease in emergence (Lookout Pass

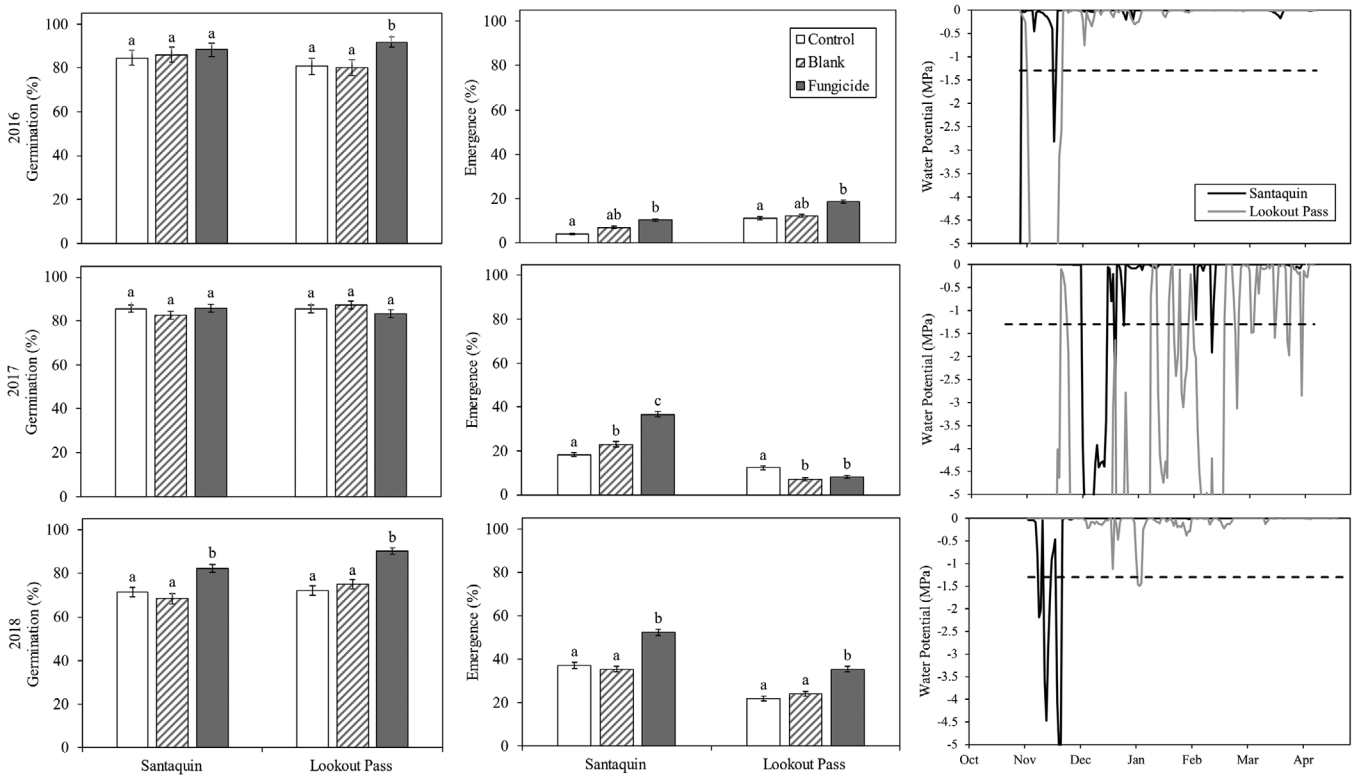

FIGURE 3 Average germination percentages (left), emergence percentages (middle) and soil water potential 2 cm below the surface (right) across all treatments, sites and years. For the germination and emergence figures, error bars represent the standard error and letters denote significant differences ($P < 0.05$). For the water potential figures, the dashed line denotes the water potential threshold for bluebunch wheatgrass germination (−1.3 MPa) and delimits the period between the seeding date and the emergence count date

2017; $P = 0.042$) to a 150.9% increase in emergence (Santaquin 2016; $P = 0.004$; Figure 3). The effect of the blank coating varied by site and year, as it performed similarly to the control in four of the six (66.7%) sites and years and similarly to the fungicide coating in three of the six (50.0%) sites and years (Figure 3). Notably, at Lookout Pass, in 2017, the blank coating and the fungicide coating decreased emergence compared to the control but were similar to each other (Figure 3).

3.3 | Cost analysis

The commercial costs of control seed and fungicide-coated seed were estimated to be \$11.18 and \$13.98 kg^{-1}, respectively (Table 3). Thus, the fungicide coating increased direct costs by approximately 25.0%. However, a weighted average of 17.5% of control seeds emerged, compared to 26.9% of fungicide-coated seeds. Thus, on average, the fungicide coating increased the emergence percentage by an average of 54.0% under the study conditions. Dividing the costs of each treatment by their respective emergence percentages, the effective cost of control seed and fungicide-coated seed was \$64.03 and \$51.99 kg^{-1}, respectively. Thus, the fungicide treatment decreased the effective cost by an estimated 18.8%. Separating the analysis by site, the fungicide coating decreased the effective cost by an estimated 25.0% in Santaquin and 9.0% in Lookout Pass. Holding all else constant at the estimated values, the fungicide treatment was economically viable when the treatment effect was above 25.0%, the treatment cost was below \$6.03 kg^{-1} seed or the seed cost was above \$5.18 kg^{-1} (Figure 4).

4 | DISCUSSION

The success of seed-based restoration efforts in dryland settings largely depends on the critical demographic period between germination and emergence (James et al., 2011, 2019; Hardegree et al., 2020). We hypothesized that fungal seed and seedling pathogenesis contribute to this bottleneck and that fungicide seed coatings would increase emergence by reducing fungal pathogenesis. Across two sites and three years, we found that most of the control seeds germinated (weighted average of 80.0%) but relatively few emerged (weighted average of 17.5%), which confirmed a strong emergence bottleneck in our study. We further found that fungicide seed coatings substantially increased emergence (by 54.0% on average), but relatively negligibly increased germination (by 8.8% on average; Figure 3). This disparity in effect size supports our hypothesis that fungal pathogens contributed to the emergence bottleneck. The fungicide coating also significantly increased emergence in five of the six sites and years, which supports our hypothesis that fungicide seed coatings would constitute an effective strategy for increasing emergence. Furthermore, our cost analysis

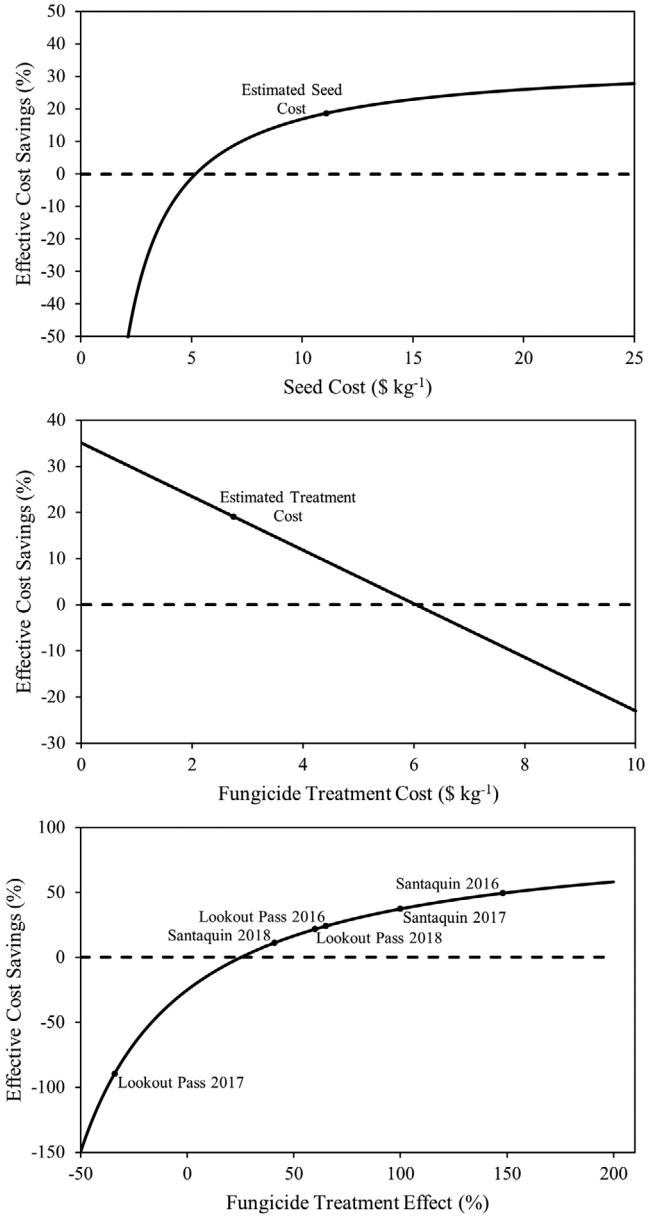

FIGURE 4 Effective cost savings given varying seed costs (top), fungicide treatment costs (middle) and fungicide treatment effects (bottom). Effective cost savings is defined as the percent difference between the cost of fungicide-coated seed and the cost of control seed with each divided by its respective emergence percentage estimate. For each analysis, all variables except the variable of interest were fixed at their respective estimates (i.e. emergence of control seed: 17.5%, emergence of fungicide-coated seed: 26.9%, seed cost: \$11.18 kg^{-1}, and fungicide treatment cost: \$2.80 kg^{-1} seed). The intersections between dashed and solid lines denote the break-even points

indicated that fungicide seed coatings were economically viable under the study conditions.

The effect of the fungicide coating on emergence was highly dependent on the year and the site, as indicated by strong interaction terms (Figure 3). It is likely that these interacting effects were largely attributable to differences in microsite conditions as influenced by such factors as seasonal weather variation, soil heterogeneity and microbial community dynamics (Blaney & Kotanen, 2001; Ehlert et al., 2014; Connolly & Orrock, 2015; Lamichhane et al., 2018; Hardegree et al., 2016; Hardegree et al., 2020). One way that weather could influence seed and seedling disease severity is by affecting germination timing and growth of both plants and pathogens (Allen et al., 2018; Lamichhane et al., 2018; Hardegree et al., 2020). Germination and growth rates of plants and fungal pathogens are proportional to the amount that temperature and water potential exceed a threshold value (Allen et al., 2018; Barth et al., 2015; Bradford, 2002; Hardegree et al., 2018). Because threshold values and response rates are diverse and unique to individual species, it is likely that seeds and pathogens respond differently to microsite temperature and water potential (Allen et al., 2018; Lamichhane et al., 2018; Richardson et al., 2018; Hardegree et al., 2020). Following the race for survival model for seed pathogenesis, the relative responses of seeds and pathogens to the hydrothermal environment regulate processes of pathogenesis and escape (Beckstead et al., 2007). The hydrothermal environment in small windows of time may favour fungal growth and pathogenesis or seed germination, growth and escape, thereby driving disease severity and the observed interactions (Allen et al., 2018; Franke et al., 2014).

The impact of the microsite hydrothermal environment on seed and seedling disease severity is further complicated by microbial community dynamics. Multiple species of graminoid pathogens are associated with bluebunch wheatgrass seed under field conditions, each of which may or may not be pathogenic to bluebunch wheatgrass (Gornish et al., 2015). Thus, it is likely that the pathogenesis of bluebunch wheatgrass seed and seedlings is not a monospecific process, but rather a process involving a community of microbes, some of which may form synergistic relationships (e.g. commensal–pathogen or pathogen–pathogen) affecting disease severity (Lamichhane & Venturi, 2015; Lamichhane et al., 2018; Mackin et al., 2021). Such systems, appropriately termed disease complexes, are common in wildland settings (Lamichhane & Venturi, 2015). Microbial communities and disease complexes can be highly sensitive to the hydrothermal environment and other stochastic ecological processes (Aanderud et al., 2013; Lamichhane & Venturi, 2015; Lamichhane et al., 2018; Mackin et al., 2021). Thus, the compositions of disease complexes affecting seeds and seedlings in this study were likely unique to each site and year to some degree. It follows that the dynamics of the microsite microbial community and disease complex could have drastically affected disease severity and the treatment interactions observed in this study.

One of the most apparent sources of the strong interaction between the site, year and treatment on emergence was that both the blank and the fungicide coatings resulted in lower emergence than the control but similar emergence to each other at Lookout Pass in 2017 (Figure 3). This pattern was unique to Lookout Pass 2017 and coincided with extraordinarily low water potentials during the winter relative to the other sites and years (Figure 3). With the exception of Lookout Pass 2017, all sites and years maintained soil water potentials above −1.3 MPa, a threshold for bluebunch wheatgrass germination (Hardegree et al., 2003), for more than 75% of the winter incubation period. By contrast, only 21% of the winter incubation period was

characterized by soil water potentials above −1.3 MPa at Lookout Pass in 2017 (Figure 3). Furthermore, Lookout Pass 2017 experienced extreme fluctuations in water potential during the winter months compared to the other sites and years (Figure 3). The dry and variable soil conditions of Lookout Pass 2017 were likely a result of abnormally low precipitation, as compared to the 30-year normal, in October through January (Figure 2). Because the blank and the fungicide coatings performed similarly, we infer that the deleterious treatment effect was due to their common thick coating. As was demonstrated in the laboratory trial, the seed coating slowed germination (Table 4). This was likely due to an increased water potential threshold required for imbibition. Assuming the delay in germination caused by the seed coating was a function of imbibition, the effect of the coating would have been exacerbated by the exceptionally dry conditions at Lookout Pass in 2017. Such a delay in germination could have extended emergence past our count date (Boyd & James, 2013).

Although germination timing may explain the deleterious effect of the seed coating on emergence at Lookout Pass in 2017, it fails to explain why the fungicide coating did not compensate for the reduced emergence by increasing survival compared to the blank coating. This lack of a positive treatment effect suggests that fungal pathogenesis was not a strong limiting factor to seedling emergence at Lookout Pass in 2017. The exceptionally dry conditions at Lookout Pass in 2017 may have reduced disease severity by impeding growth and pathogenesis of the most important disease complexes at a higher rate than the growth and escape mechanisms of bluebunch wheatgrass through a variety of individual and community scale mechanisms (Lamichhane & Venturi, 2015; Lamichhane et al., 2018). Such interactions between the microsite hydrothermal environment and microbial community dynamics and processes are highly complex. Further research is necessary to fully understand how these interactions influence seed and seedling disease severity, plant phenology and restoration success. Additional research is also necessary to integrate these concepts into the context of a changing climate (Connolly & Orrock, 2015; Lamichhane et al., 2018).

Robust cost analyses for ecological restoration are notoriously difficult to perform and are usually omitted from scientific publications due to complications such as varying costs across space, time and project scale, hidden costs, subjectivity surrounding definitions of restoration success and stochastic processes involved in restoration outcomes (Kimball et al., 2015; Pedrini et al., 2020; Bodin et al., 2021). The limitations to our cost analysis reflect these complications. First, estimates of seed and treatment costs were based on personal communications, although costs to practitioners may vary considerably. For this reason, we evaluated the economic viability of the treatment across a range of seed and treatment costs (Figure 4). Second, only the seed treatment phase of the restoration process was considered, although seed-based restoration also involves costs associated with preparing the site for seeding, sourcing seed, delivering seed, monitoring and other facets (Erickson & Halford, 2020; Shaw et al., 2020). Third, seeding success was defined by emergence, although restoration goals may include improving ecosystem services, such as livestock forage or reduced fire risk, developing habitat or matching a reference condition (Kimball et al., 2015; Shackelford et al., 2021). However, because emergence is often the most important bottleneck in seed-based restoration, it often correlates with other metrics of success (James et al., 2011, 2019; Kimball et al., 2015; Hardegree et al., 2020). Finally, fungicide treatment effectiveness may vary by restoration species, morphology and phenology, site, weather, microbial community dynamics and their interactions, as was the case in this study (Allen et al., 2018; Lamichhane & Venturi, 2015; Lamichhane et al., 2018; Mackin et al., 2021). Despite these limitations, cost analyses are essential if effective treatments are to be applied by practitioners (Kimball et al., 2015; Pedrini et al., 2020; Bodin et al., 2021).

Based on emergence counts and cost estimates, the fungicide seed coating constituted an economically viable seed treatment across both sites and at each site individually. However, the fungicide coating was not economically viable in each site and year (i.e. Lookout Pass 2017; Figure 4). Therefore, it may be expected that fungicide coatings would not be economically viable in every restoration setting, but long-term averages may result in considerable net savings. Indeed, even relatively small savings may have large consequences over the large spatiotemporal scales typical of dryland restoration. Furthermore, cost savings increase relative to the price of the seed, and therefore may have large consequences for rare or otherwise expensive seed species (Figure 4). Although this study involved only one species, two sites and three years, and therefore is not fully representative of the diversity of dryland restoration scenarios, it provides evidence that fungicide seed coatings have the potential to cost-effectively improve restoration seeding success. Future research is merited to explore the use of fungicides with other species in other settings, particularly in species without dormancy periods and post-fire or other disturbance.

Before fungicide seed coatings can be widely adopted for restoration use, they should be thoroughly tested for deleterious environmental effects, a process which is required in many countries under environmental legislations such as the Environmental Protection Act. This process would include a thorough investigation of the risks of fungicide use to humans, wildlife, fish, plants and other non-target organisms, as well as surface and groundwater contamination in a variety of restoration contexts. Although these risks were investigated prior to registration for agricultural use, some risks may be of higher concern in restoration settings. For example, the risk of fungicides to beneficial microorganisms, particularly mycorrhizae, is likely more important when seeding perennial restoration species that will experience summer drought than when seeding irrigated annual agricultural species. The effects of fungicide seed coatings on mycorrhizae are diverse, understudied and complicated by a myriad of variables, including the mobility and mode of action of fungicide, the plant species, the microbial community and their interactions (Cameron et al., 2017). However, non-target effects may be mitigated by the highly localized nature of seed coatings and the short half-lives of most fungicides relative to the incubation period of fall-planted restoration species (Jin et al., 2013; Cameron et al., 2017; Table 1). Given the positive results of fungicide use in this study, investigation of the potential non-target effects of fungicide seed coatings

and registration of fungicides for restoration use, if appropriate, could be highly beneficial.

Using bluebunch wheatgrass as a model species, we demonstrated that fungicide seed coatings have the potential to cost-effectively improve the probability of emergence in dryland restoration seedings. The success of fungicide seed coatings in this study and agriculture provides promising evidence that fungicides may be used to improve seeding success. Future research should explore the effects of fungicide seed coatings on other species and in other biomes where fungal pathogenesis is limiting restoration success. Further research should also explore the interrelated concepts of hydrothermal accumulation, the race for survival and disease complexes as these may drive disease severity. Exploring the effects of fungicides over a larger sample of species and sites and understanding the ecological processes driving interactions would allow for a higher degree of inference and improve our ability to determine the conditions under which fungicides are likely to be cost-effective. Overall, fungicide seed coatings are a promising tool for future restoration application.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

MM conceived the research. MM and WR developed the seed coating and conducted the laboratory trials. BH, WR and MM designed and implemented the field trials. MM compiled cost estimates. BH conducted the statistical analysis and wrote the manuscript. All authors provided critical feedback throughout the study and refined the manuscript.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.0gb5mkm2x (Hoose et al., 2022).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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