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RESEARCH ARTICLE

Integrating herbicide application and seeding techniques to restore native plant diversity in crested wheatgrass-dominated rangelands

Peter Bugoni[1,2], Jane Mangold[3]

Abstract

Introduction: Restoring native plant diversity in crested wheatgrass (*Agropyron cristatum*)-dominated rangelands is a persistent challenge in ecological restoration across western North America. Dense, long-lived stands of this exotic grass suppress native seedling recruitment, hinder habitat restoration, and reduce ecosystem resilience. Identifying herbicide and seeding strategies that enhance native establishment is therefore critical for improving rangeland restoration outcomes.

Objectives: We evaluated whether herbicide intensity, seeding configuration, and their interaction influenced suppression of *A. cristatum*, establishment of seeded native grasses and forbs, and shifts in plant community composition across three crested wheatgrass-invaded sites.

Methods: We applied glyphosate at low (1.1 L/ha) and high (2.3 L/ha) rates, plus an unsprayed control, combined with two drill-seeding configurations across three crested wheatgrass-invaded sites in Montana. Each site was drill-seeded with six native grasses and six native forbs; vegetation was sampled in late June to early July in each year following treatment. Cover, density, and community composition were analyzed for all treatment combinations.

Results: Higher glyphosate intensity consistently reduced *A. cristatum* cover across sites. Seeded native grasses showed modest increases under some herbicide–seeding combinations, while seeded forb establishment remained low. Community analyses indicated significant treatment effects, with herbicide intensity contributing more strongly to shifts in community composition than seeding configuration.

Conclusions: Pre-seeding herbicide applications reduced *A. cristatum* dominance and modestly improved native grass establishment, but forb establishment remained limited under all treatments. Across sites, herbicide intensity was a stronger driver of early restoration response than seeding configuration.

Implications for Practice: For land managers, our results suggest that prioritizing effective suppression of *A. cristatum* is essential to improving opportunities for native species establishment. Higher glyphosate rates produced stronger reductions in *A. cristatum* and contributed more to shifts in community composition than seeding configuration. However, forb establishment remained low, indicating that additional interventions beyond suppression and standard seeding may be needed to restore diverse forb communities in *A. cristatum*-invaded rangelands, including modified seedbeds, repeated herbicide applications, and targeted forb restoration strategies.

Key words: alternate-row and cross-seeding, ecological restoration, glyphosate, native species establishment, plant community assembly, rangeland management

Introduction

Few rangeland interventions have been as successful, or as consequential, as the deliberate seeding of crested wheatgrass across the Intermountain West. Introduced from Eurasia in the early 20th century, *Agropyron cristatum* (L.) Gaertn. and *A. desertorum* (Fisch. ex Link) Schult. were rapidly adopted as a forage improvement grass by federal agencies and land managers (Mayland et al. 1992; Sayre 2017). Its early spring growth, cold and drought hardiness, and ease of establishment under harsh conditions made it reliable on working rangelands under grazing pressure (USDA-NRCS 2001; Sheley et al. 2008). Millions of hectares of native grassland were converted to *A. cristatum* stands through the mid-20th century, producing communities that delivered on their agronomic promise but displaced the native diversity they replaced (McAdoo et al. 1989).

Agropyron cristatum-dominated communities lack the structural and floristic diversity necessary to support many wildlife

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species (McAdoo et al. 1989). Sagebrush-obligate species such as the greater sage-grouse (*Centrocercus urophasianus*), for example, depend on diverse plant communities that sustain insect abundance critical to chick survival (Gregg et al. 2008). Monotypic stands also alter belowground processes. *Agropyron cristatum* produces lower root biomass and contributes less organic matter than co-occurring native grasses, reducing soil organic matter, increasing bulk density, and altering nutrient cycling (Biondini et al. 1988; Redente et al. 1989; Dormaar et al. 1995; Lesica & DeLuca 1996). These soil conditions inhibit native species establishment and reinforce *A. cristatum* dominance.

Despite widespread interest in reducing *A. cristatum* dominance, prior herbicide applications have produced inconsistent and often short-lived suppression. Wilson and Partel (2003) achieved only partial suppression at 1.1 kg active ingredient (a.i.)/ha with rapid regrowth requiring repeated mechanical treatments. Subsequent studies reinforced this pattern: Fansler and Mangold (2011) documented increases rather than decreases in *A. cristatum* density following glyphosate application with disking; Hulet et al. (2010) found that higher rates (3.2 L/ha) produced stronger initial reductions but stands rebounded to pretreatment levels within 2–3 years; and McAdoo et al. (2017) reported only temporary control across multiple herbicide chemistries before *A. cristatum* rapidly regained dominance. Suppression without addressing the competitive and belowground feedbacks maintaining *A. cristatum* dominance appears inherently temporary.

Suppression and native establishment are related but distinct problems. Herbicide applications at commonly used rates have generally been insufficient to reduce *A. cristatum* competitive pressure long enough to facilitate native recruitment, and low-disturbance revegetation approaches frequently fail when suppression is inadequate (Morris et al. 2019). Disturbance-driven resource pulses increase community invasibility, but only when propagule pressure and establishment conditions favor the incoming species (Davis et al. 2000). Even when herbicide creates temporary resource availability, those windows may close before seeded species can capitalize on them (Jefferson et al. 2021). This challenge is most acute for forbs, where priority effects and early grass competition can suppress recruitment even when the dominant competitor is reduced (Fukami 2015; Young et al. 2017).

Seeding grasses and forbs in separate drill passes reduces the competitive head start that faster-establishing grasses would otherwise exert over forbs during early recruitment, offering a potential solution to the forb establishment bottleneck (Porensky et al. 2012; Pokorny et al. 2020). Spatial seeding addresses the recruitment bottleneck directly, but the belowground legacy effects of *A. cristatum* and the insufficiency of suppression at commonly used rates suggest that no single intervention is sufficient. These reinforcing feedbacks are consistent with an alternative stable state maintained by vegetation, soil, and disturbance dynamics that resist single-factor interventions (Suding et al. 2004; Hobbs & Suding 2009). Overcoming them likely requires paired interventions that achieve strong competitive release while directing establishment toward desired species rather than opportunistic colonizers (Chang et al. 2019; Hanusch et al. 2022). Building on prior research, we implemented three herbicide treatments (control, low, and high glyphosate rates) and two drill-seeding configurations (combined vs. separate) across three *A. cristatum*-dominated sites in Montana to evaluate whether stronger suppression and spatial seeding strategies can improve restoration outcomes. Our objectives were to determine whether (1) glyphosate application rate influences the magnitude of *A. cristatum* suppression, (2) herbicide intensity affects the establishment of seeded native grasses and forbs, and (3) seeding grasses and forbs in separate drill passes improves establishment compared to seeding them together. We hypothesized that higher glyphosate rates would yield greater suppression of *A. cristatum*; that seeded native grasses and forbs would establish at higher densities under high-rate treatments; and that separating functional groups during seeding would increase establishment by reducing early interspecific competition.

Methods

Site Descriptions

This study was conducted at three sites in Montana, USA, dominated by *A. cristatum*: the Northern Agriculture Research Center (NARC), Berry Farm, and Pine Butte Preserve (PBP).

NARC is a 13.3-ha site near Havre, MT (48.4947°N, −109.8164°W) at 792 m elevation on level terrain. Soils derived from the Hillon series (Aridic Haplustepts) consist of clay loams (Soil Survey Staff 2024). Classified as loamy dry grassland within the Brown Glaciated Plains MLRA (USDA-NRCS 2022), the region receives 25–35 cm of annual precipitation, primarily in late spring and early summer. The site was farmed until 1994, then seeded to non-native perennial grasses and subsequently grazed annually.

Berry Farm is a 13-ha site northwest of Sidney, MT (47.8629°N, −104.2639°W), situated on 2–8% slopes at 673 m elevation. Soils consist of loams of the Williams series (Typic Argiustolls) (Soil Survey Staff 2024). Located in the Glacial Till Plains MLRA, the region receives 28–33 cm of precipitation annually (USDA-NRCS 2022). The site was in wheat–fallow rotation until 1965, then seeded to *A. cristatum* and alfalfa (*Medicago sativa*) and used for hay, followed by periodic short-duration grazing.

PBP is a 14.5-ha level site west of Choteau, MT (47.8267°N, −112.5607°W) at 1,400 m elevation. Soils consist of Aquic Calciborolls derived from clay loams (Soil Survey Staff 2024). The site lies within the Northern Rocky Mountain Foothills MLRA, receiving 46–51 cm of annual precipitation (USDA-NRCS 2022). Seeded to *A. cristatum* and historically flood-irrigated for hay until the early 1980s, the site has since been managed with spring grazing.

Pre-Treatment Sampling

Prior to herbicide application, *A. cristatum* cover was quantified at each site in spring 2018 using a stratified random sampling design. Thirty points were generated within each site using

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ArcGIS Pro (ESRI, Redlands, CA, U.S.A.). At each point, two perpendicular 25-m transects intersecting at the point center defined four quadrants. A 1 × 0.5 m quadrat was tossed into each quadrant, and crested wheatgrass cover was visually estimated to the nearest 1%. Values were averaged across quadrants; descriptive statistics summarizing pre-treatment conditions are provided in Table S1.

Experimental Design

At each site, glyphosate was applied at three rates (control: unsprayed; low: 1.1 L/ha, 96 oz/acre; high: 2.3 L/ha, 192 oz/acre) and factorially combined with two drill-seeding configurations, combined and separate. In the combined treatment, all species were seeded in a single drill pass. In the separate treatment, grasses and forbs were seeded separately in perpendicular drill passes following Scianna et al. (2014). Each treatment combination was replicated three times per site in a completely randomized design. Plots measured 130 m × 60 m.

Herbicide Application

Herbicide applications were conducted shortly before seeding and followed site-specific protocols. At NARC, glyphosate was applied in mid-April 2020 using a 9-m boom equipped with TeeJet® flat-fan nozzles spaced 50 cm apart and mounted at 76 cm height; spray volume was 16 L/ha at 6.5 kph. At Berry Farm, herbicide was also applied in mid-April 2020 using a 12-m boom with TeeJet® even-banding nozzles (50-cm spacing; 50-cm height), also at 16 L/ha and 6.5 kph. At PBP, glyphosate was applied in early May 2021 using UTV-mounted Boominator® spray tips set at 76 cm height, applying 8 L/ha at 8 kph.

Seeding

Each site was seeded with six native grasses and six native forbs at pure live seed (PLS)-adjusted rates. Four species (*Astragalus canadensis*, *Gaillardia aristata*, *Ratibida columnifera*, and *Pascopyrum smithii*) were common to all sites; remaining species differed by site (Table 1). PLS values were provided by the seed supplier and are reported in Table S2. Site-specific seeding densities ranged from 0.19 to 1.9 kg/ha for grasses and 0.09 to 1.1 kg/ha for forbs. Rice hulls were added at 55% volume to ensure uniform seed flow. NARC and Berry Farm were seeded using a Truax FlexII no-till drill (20-cm row spacing; 1.2-cm depth) on 11 and 18 May 2020, respectively. PBP was seeded using a Haybuster® 10C drill (18-cm row spacing; 1.3-cm depth) on 7 June 2021.

Vegetation Sampling

Vegetation was sampled at NARC and Berry Farm in late June to early July of 2020, 2021, and 2022. At PBP, herbicide and seeding treatments were implemented in 2021; vegetation was therefore sampled in late June to early July of 2021 and 2022 only. Within each plot, three permanent 100-m transects were established lengthwise along the 130-m axis, spaced 20 m apart and positioned 10 m from plot edges. At 10-m intervals along each transect, a 1 × 0.5 m quadrat was placed, producing 10 quadrats per transect and 30 quadrats per plot.

Within each quadrat, percent cover was visually estimated to the nearest 1% for all species present. Species were subsequently assigned to one of four groups for analysis: *A. cristatum*, seeded native grasses, seeded native forbs, and other species (all nonseeded species combined). For density, grass tillers and individual forb plants were counted.

Statistical Analysis

All univariate analyses were conducted separately for each site. Percent cover of crested wheatgrass, seeded grasses, seeded forbs, and other species was analyzed using beta regression models implemented in the glmmTMB package (Brooks et al. 2017). Cover values were scaled to fall within 0.1. Seeded grass and forb densities were analyzed using negative binomial generalized linear mixed-effects models (also fitted with glmmTMB), with zero inflation incorporated where diagnostics indicated excess zeros and dispersion structures modified when needed to improve fit. For both model types, fixed effects included herbicide treatment, seeding method, sampling year, and their interactions, and plot and transect nested within plot were included as random intercepts.

All models were evaluated using DHARMa (Hartig 2022) to assess residual structure, dispersion, zero inflation, and overall model fit. Post hoc comparisons were conducted using estimated marginal means with Tukey adjustments in the emmeans package (Lenth 2022) and reported on the response scale. Statistical significance was evaluated at $\alpha = 0.05$. Full model results including type III Wald χ^2 statistics for all fixed effects are provided in Table S3.

Community-level responses were analyzed using permutational multivariate analysis of variance (PERMANOVA; adonis2 in the vegan package; Oksanen et al. 2022) applied to Bray–Curtis dissimilarities of quadrat-level species abundance. Abundances were square-root transformed prior to analysis to reduce the influence of dominant species. Homogeneity of multivariate dispersion was assessed using permutation-based tests of beta dispersion (betadisper and permutest in the vegan package), with post hoc Tukey contrasts, to evaluate whether PERMANOVA results could be attributable to differences in within-group dispersion rather than among-group centroid differences. NMDS ordinations were computed on background species only, excluding *A. cristatum*, seeded grass, and seeded forb cover, to visualize compositional turnover among nonfocal taxa independent of the dominant treatment-responsive species; the full species matrix including those focal groups was used for PERMANOVA. All figures were created in ggplot2 (Wickham 2016), and all analyses were conducted in R 4.3.2 (R Core Team 2023). PERMANOVA results by term for all sites are provided in Table S4.

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Table 1. Seeded grass and forb species and associated seeding rates in pure live seed (PLS) at Crested Wheatgrass study sites. "X" indicates seeded at site.

Species (Common Name and Scientific Name) *Grasses*	*NARC*	*Berry Crested*	*PBP*
Blue grama	X	X	
Bouteloua gracilis	0.38 kg/ha	0.38 kg/ha	
Bluebunch wheatgrass	X	X	
Pseudoroegneria spicata	1.3 kg/ha	1.3 kg/ha	
Green needlegrass	X	X	
Nassella viridula	1.1 kg/ha	1.1 kg/ha	
Prairie junegrass	X		
Koeleria macrantha	0.19 kg/ha		
Sideoats grama	X	X	
Bouteloua curtipendula	1.1 kg/ha	1.1 kg/ha	
Western wheatgrass	X	X	X
Pascopyrum smithii	1.9 kg/ha	1.9 kg/ha	1.9 kg/ha
Slender wheatgrass		X	X
Elymus trachycaulus		0.26 kg/ha	0.26 kg/ha
Basin wildrye			X
Elymus cinereus			1.3 kg/ha
Beardless wildrye			X
Elymus triticoides			1.3 kg/ha
Canada wildrye			X
Elymus canadensis			1.5 kg/ha
Prairie cordgrass			X
Spartina pectinata			1.1 kg/ha
Forbs	*NARC*	*Berry Crested*	*TNC*
Blanket flower	X	X	X
Gaillardia aristata	1.1 kg/ha	1.1 kg/ha	1.1 kg/ha
Prairie coneflower	X	X	X
Ratibida columnifera	0.38 kg/ha	0.38 kg/ha	0.38 kg/ha
Purple prairie clover	X	X	
Dalea purpurea	0.7 kg/ha	0.7 kg/ha	
Canada milkvetch	X	X	X
Astragalus canadensis	0.8 kg/ha	0.8 kg/ha	0.8 kg/ha
Missouri goldenrod	X	X	X
Solidago missouriensis	0.2 kg/ha	0.2 kg/ha	0.2 kg/ha
Scarlet globemallow	X	X	
Sphaeralcea coccinea	0.38 kg/ha	0.38 kg/ha	
Western yarrow			X
Achillea millefolium			0.09 kg/ha
Boreal sweetvetch			X
Hedysarum boreale			1.1 kg/ha

Results

A. cristatum cover responded strongly to herbicide application rate across all sites, with significant herbicide × year interactions at Berry Farm, NARC, and PBP (all $p < 0.0001$; Fig. 1). A consistent pattern emerged: high and low glyphosate rates suppressed *A. cristatum* far more effectively than the control, and suppression was most pronounced in the earliest post-treatment year.

High plots had the lowest *A. cristatum* cover at Berry Farm in 2020 (7%, 95% CI: 5–9) and remained suppressed in 2021–2022. Low plots exhibited intermediate suppression, while control plots had the greatest cover early in the study. However, by 2022 control cover declined to levels comparable to low plots (Fig. 1). At NARC, *A. cristatum* cover in high plots remained near zero across all years (<1%), while low plots maintained low cover (1–6%). In contrast, control plots retained moderate cover that increased over time (24% in 2020; 34% in 2021; 41% in 2022; Fig. 1). At PBP, herbicide suppression was most dramatic. High and low plots exhibited near-complete elimination of *A. cristatum* in both 2021 and 2022 (0–1%), whereas control plots maintained very high cover in 2021 (58%, 95% CI: 54–62) before declining to 36% (95% CI: 32–39) in 2022 (Fig. 1). Across sites, seeding method did not significantly influence *A. cristatum* cover.

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Seeded forb density responded to glyphosate rate across sites, with a significant three-way interaction among herbicide, seeding method, and year at Berry Farm ($p < 0.001$), a significant herbicide × year interaction at NARC ($p < 0.0001$), and a significant three-way interaction at PBP ($p < 0.0001$; Fig. 2).

At Berry Farm, seeded forb density exhibited a three-way interaction of herbicide, seeding method, and year. Forb density was highest in 2020 and declined thereafter, but herbicide-treated plots consistently supported greater establishment than control plots (Fig. 2). Seeding method effects were apparent at Berry Farm. Separate seeding combined with the high herbicide rate produced the highest forb densities, whereas combined seeding often resulted in lower establishment under the same herbicide treatments. These seeding method contrasts were most

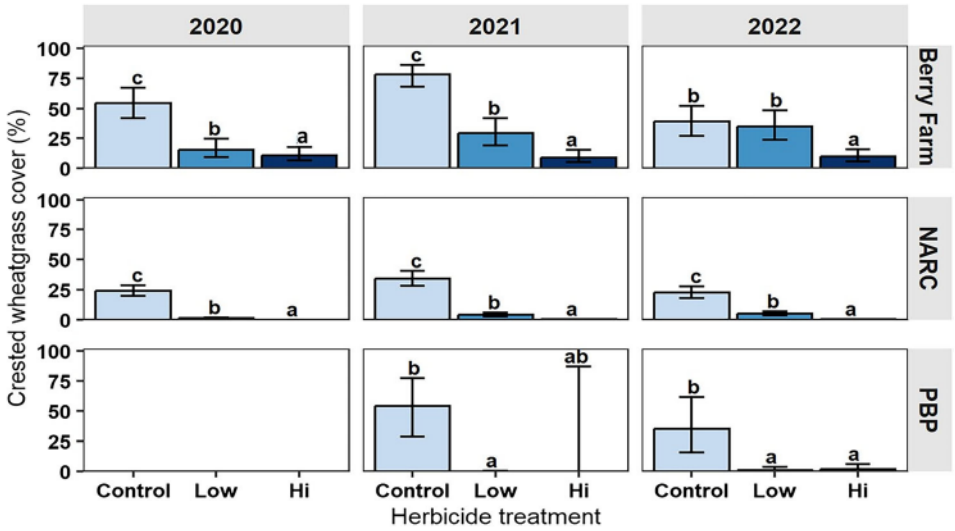


Figure 1. *Agropyron cristatum* cover (%) in response to herbicide treatment across three sites and years. PBP was not sampled in 2020. At NARC and Berry Farm, cover was modeled using beta regression GLMMs; at PBP, a betabinomial GLMM was used to accommodate the high frequency of zero-cover quadrats in herbicide-treated plots. The wide confidence interval and intermediate letter grouping for the high treatment at PBP in 2021 reflect near-complete suppression and associated model uncertainty. Bars show back-transformed estimated marginal means with 95% CI; letters denote Tukey-adjusted pairwise differences within each site × year panel ($\alpha = 0.05$).

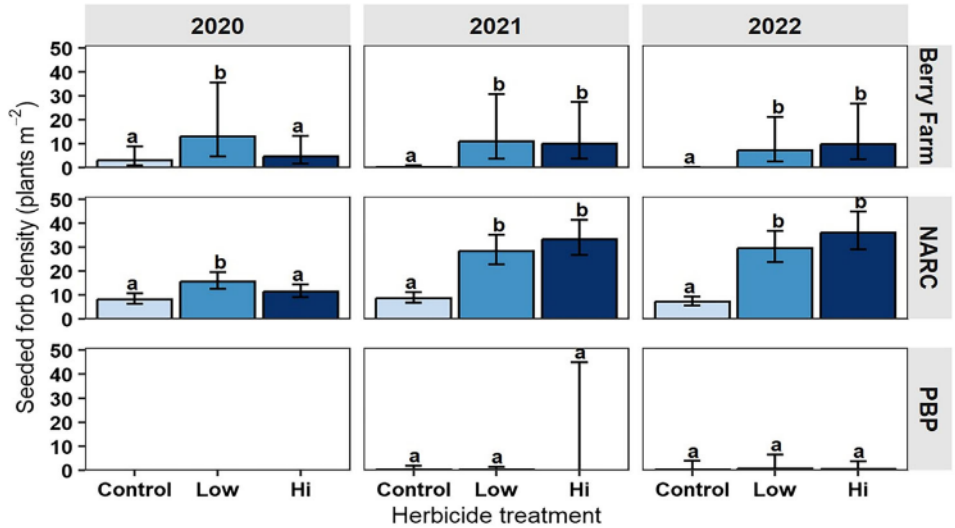


Figure 2. Seeded forb density (plants m^{-2}) in response to herbicide treatment across three sites and years. PBP was not sampled in 2020. At NARC and Berry Farm, densities are derived from negative binomial GLMMs with herbicide × year × seeding method interaction terms; bars show emmeans averaged over seeding method. At PBP, densities reflect herbicide × year effects only. The wide confidence interval for the high treatment at PBP in 2021 reflects near-zero observed densities and high model uncertainty. Bars show back-transformed estimated marginal means with 95% CI; letters denote Tukey-adjusted pairwise differences within each site × year panel ($\alpha = 0.05$).

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apparent in 2020 and 2021 and diminished slightly by 2022. At Berry Farm in 2022, the low treatment did not differ significantly from control plots in forb density. At NARC, forb density increased in herbicide-treated plots following application. In 2020, density in the low treatment exceeded control plots, while high did not differ significantly from control. By 2021 and 2022, both low and high treatments exceeded control, and densities in herbicide-treated plots increased from 2020 to 2021 and remained stable in 2022, whereas control densities stayed low (approximately 5 plants m^{-2}, 95% CI: 4–8) across all years (Fig. 2). At PBP, seeded forb establishment was uniformly low across treatments and predicted densities remained near zero. Herbicide treatments did not produce consistent increases in forb density relative to controls, and densities exhibited small fluctuations across herbicide and seeding treatments without clear treatment-based patterns (Fig. 2).

Seeded grass density responded to herbicide treatments at Berry Farm and NARC, though the form and magnitude of the response differed between sites. At PBP, grass density remained low regardless of treatment. At Berry Farm, seeded grass density varied by herbicide × year ($p = 0.0033$). Densities were lowest in control plots across all years, remaining below 1 tiller m^{-2} (2020–2022; Fig. 3). In 2020, low and high treatments showed modest establishment. By 2021, densities increased in treated plots, and by 2022, establishment was highest in herbicide-treated areas (low: ≈41 tillers m^{-2}; high: ≈19 tillers m^{-2}), with control plots remaining near zero (Fig. 3). At NARC, grass density exhibited a significant herbicide × year interaction ($p < 0.0002$). In 2020, densities were highest in control plots (approximately 34 tillers m^{-2}) and were lower in low and high treatments (Fig. 3). By 2021, densities in low and high plots increased and were more similar to control plots (control: ≈17 tillers m^{-2}; low: ≈14 tillers m^{-2}; high: ≈5 tillers m^{-2}). In 2022, herbicide-treated plots exhibited the greatest densities, surpassing the control; this temporal pattern reflects low initial establishment in treated plots followed by sharp increases through time (Fig. 3). At PBP, seeded grass density was extremely low across treatments and years, consistent with limited establishment at this site. Grass densities in 2021 were low across treatments and in 2022, densities remained low in the control (≈0.6 tillers m^{-2}), increased modestly in the low treatment (≈4.2 tillers m^{-2}), and remained low in high (≈0.8 tillers m^{-2}) (Fig. 3). Seeding method did not significantly influence seeded grass density at any site.

Other species cover showed higher-order interactions involving herbicide treatment, seeding method, and year at most sites. At Berry Farm, other species cover showed a three-way herbicide × seeding × year interaction ($p = 0.0004$). Cover was highest in 2020 and declined thereafter. Within the combined seeding method in 2020, high plots had the greatest other species cover (≈14%, 95% CI: 11–17), followed by control (≈10%, 95% CI: 8–13) and low (≈6%, 95% CI: 5–8). In Separate seeding, patterns were similar but with slightly lower overall cover. By 2021 and 2022, differences among herbicide treatments were small, with all treatments converging toward low cover values (generally <4%; Fig. 4). Tukey-adjusted comparisons showed clear treatment differences in 2020 but few in 2021–2022, consistent with the overall decline in other species cover across years. At NARC, other species cover was influenced by a significant herbicide × seeding × year interaction ($p = 0.0135$). In 2020, cover was lowest in control plots and highest in herbicide-treated plots for both seeding methods.

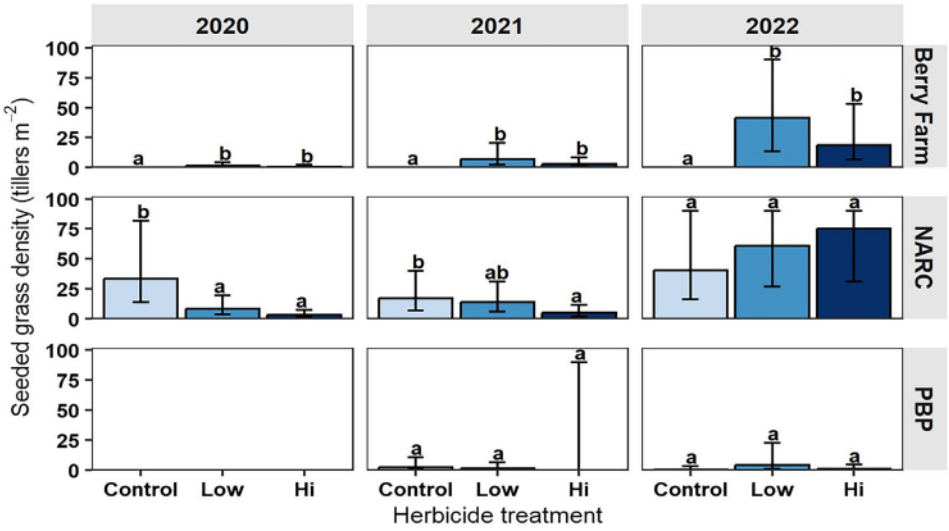


Figure 3. Seeded grass density (tillers m^{-2}) in response to herbicide treatment across three sites and years. PBP was not sampled in 2020. At NARC and Berry Farm, densities are derived from negative binomial GLMMs with herbicide × year interaction terms. At PBP, densities are derived from a simplified negative binomial model used for figure generation; inference is based on the hurdle model reported in the text. The wide confidence interval for the high treatment at PBP in 2021 reflects near-zero observed densities and high model uncertainty. Bars show back-transformed estimated marginal means with 95% CI; letters denote Tukey-adjusted pairwise differences within each site × year panel ($\alpha = 0.05$).

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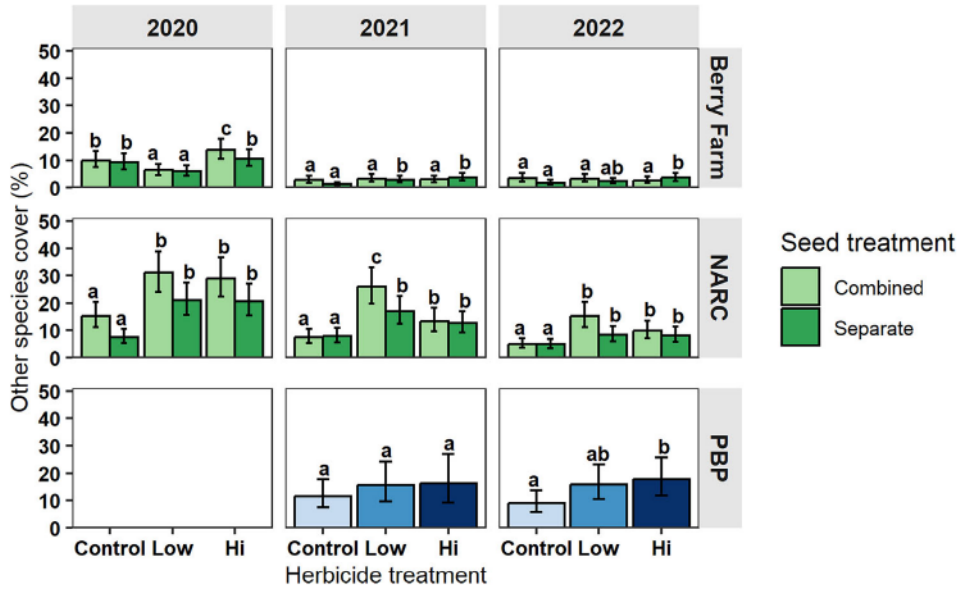


Figure 4. Other species cover (%) in response to herbicide and seeding treatments across three sites and years. At Berry Farm and NARC, cover was modeled with a three-way interaction among herbicide treatment, seeding method, and year; bars are colored by seeding method (combined and separate). At PBP, the model supported herbicide × year effects only; bars are colored by herbicide treatment (control, low, and high). PBP was not sampled in 2020. Bars show back-transformed estimated marginal means with 95% CI; letters denote Tukey-adjusted pairwise differences within each site × year panel ($\alpha = 0.05$).

Cover declined in subsequent years across all treatments (Fig. 4). By 2022, combined-seeded low and high plots maintained higher cover (≈15% and ≈10%, respectively) than control (≈5%), and this pattern was reflected similarly in separate-seeded plots (separate: low ≈8%, high ≈8%, control ≈5%). At PBP, other species cover followed a herbicide × year interaction ($p < 0.0001$). In 2021, cover was lowest in control plots (≈12%, 95% CI: 8–17) and slightly higher in low (≈16%, 95% CI: 11–23) and high (≈16%, 95% CI: 10–25) treatments, though all three treatments shared the same compact letter group (Fig. 4). By 2022, cover increased in herbicide-treated plots and decreased slightly in the control.

Herbicide treatment and year were the primary drivers of plant community composition across sites, with seeding method contributing smaller and site-dependent effects. At Berry Farm, the full model was significant ($R^2 = 0.33$, $F_{17,1471} = 42.74$, $p < 0.001$), with herbicide treatment accounting for the largest share of explained variation ($R^2 = 0.16$, $F_{2,1471} = 179.40$, $p < 0.001$) and year contributing a smaller but significant component ($R^2 = 0.08$, $F_{2,1471} = 88.12$, $p < 0.001$). Seeding method was not significant as a main effect ($R^2 = 0.003$, $p = 0.617$). The assumption of homogeneous dispersion was not met for herbicide treatment ($F_{2,1486} = 752.77$, $p < 0.001$) but was met for seeding method ($F_{1,1487} = 0.32$, $p = 0.601$), with dispersion also differing among years ($F_{2,1486} = 14.39$, $p < 0.001$), driven by lower dispersion in 2022 than in preceding years. The NMDS ordination (stress = 0.072; Fig. 5) showed clear herbicide-related clustering and modest temporal shifts, while seeding methods overlapped extensively within herbicide–year groups. At NARC, the full PERMANOVA model was significant ($R^2 = 0.38$, $F_{17,1579} = 56.96$, $p < 0.001$), with herbicide treatment accounting for the largest share of explained variation ($R^2 = 0.26$, $F_{2,1579} = 336.91$, $p < 0.001$), followed by year ($R^2 = 0.09$, $F_{2,1579} = 119.90$, $p < 0.001$) and seeding method ($R^2 = 0.01$, $F_{1,1579} = 13.73$, $p < 0.001$), with all two- and three-way interactions also significant (all $p \leq 0.003$). The assumption of homogeneous multivariate dispersion was not met for herbicide treatment ($F_{2,1594} = 323.11$, $p < 0.001$) or year ($F_{2,1594} = 149.43$, $p < 0.001$), indicating that centroid-based interpretations should be made with caution; dispersion did not differ between seeding methods ($F_{1,1595} = 3.51$, $p = 0.068$). The effect size for herbicide treatment was nevertheless large, and the NMDS ordination (stress = 0.068; Fig. 6) showed distinct herbicide-driven shifts in community composition through time. At PBP, herbicide treatment was the dominant driver of community composition ($R^2 = 0.30$, $F_{2,818} = 197.95$, $p < 0.001$), with the full model explaining 38% of variation ($R^2 = 0.38$, $F_{11,818} = 44.68$, $p < 0.001$). Year ($R^2 = 0.02$, $F_{1,818} = 27.49$, $p < 0.001$) and seeding method ($R^2 = 0.004$, $F_{1,818} = 5.80$, $p < 0.001$) each contributed smaller but significant components. The assumption of homogeneous dispersion was not met for herbicide treatment ($F_{2,827} = 24.63$, $p < 0.001$) but was met for seeding method ($F_{1,828} = 3.47$, $p = 0.064$) and year ($F_{1,828} = 3.89$, $p = 0.043$). The NMDS ordination (stress = 0.052; Fig. 7) reflected the dominant role of herbicide in structuring

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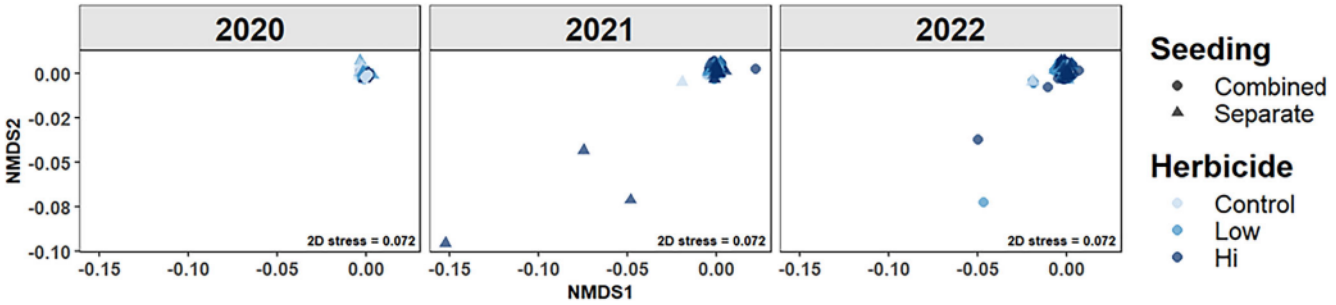


Figure 5. Two-dimensional NMDS ordination of background species community composition at Berry Farm (stress = 0.072). Points represent individual quadrat scores; herbicide treatment is indicated by color and seeding method by shape. Ellipses depict 95% confidence regions for herbicide treatment groups where point dispersion was sufficient for computation. Tight clustering of herbicide-treated quadrats near the origin in 2020 and 2022 reflects convergence on compositionally impoverished communities following glyphosate application; greater dispersion in control plots reflects background community heterogeneity.

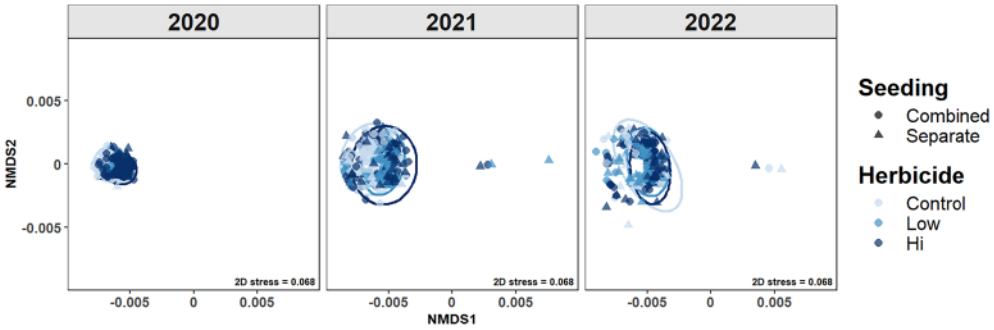


Figure 6. Two-dimensional NMDS ordination of background species community composition at NARC (stress = 0.068). Points represent individual quadrat scores; herbicide treatment is indicated by color and seeding method by shape. Ellipses depict 95% confidence regions for herbicide treatment groups where point dispersion was sufficient for computation. Control quadrats progressively diverge from herbicide-treated quadrats along NMDS1 across years, reflecting increasingly distinct background species assemblages in unsprayed plots relative to glyphosate-treated plots.

community composition, with control quadrats separating from herbicide-treated plots along NMDS1.

Discussion

Reducing *A. cristatum* dominance and establishing native species are governed by different ecological processes, and success at one does not guarantee progress toward the other. Glyphosate intensity was the primary driver of early vegetation response across all three sites. Suppression was strong, often persistent, and restructured plant community composition regardless of seeding configuration. Yet competitive release did not translate into native recovery. Seeded species, particularly forbs, established poorly under all treatments, and nonseeded species frequently colonized the space vacated by *A. cristatum*. The central obstacle is not suppression. It is recruitment.

Both glyphosate rates substantially reduced *A. cristatum* cover at all three sites, with suppression most pronounced at PBP and sustained at NARC and Berry Farm. These results are consistent with prior work showing that glyphosate can temporarily suppress *A. cristatum* (Wilson & Partel 2003; McAdoo et al. 2017), but suppression at our rates persisted across the full 3-year observation period, unlike the 2–3-year rebound documented by Hulet et al. (2010). Sustained suppression at operational scales extends prior benchmarks. Intense herbicide application can relax *A. cristatum* competitive dominance for longer than previously documented, creating a more durable window for native establishment than earlier studies indicated was possible. Even so, where suppression approached local elimination at PBP, the plant community did not transition toward native dominance. Removing a dominant competitor initiates the conditions for restoration but does not complete the transition. The barriers to native recovery are not resolved by competitive suppression alone (Hobbs & Norton 1996; Hobbs & Suding 2009).

Native grass establishment improved with herbicide treatment at NARC and Berry Farm but not at PBP, and at no site did the high rate produce greater establishment than the low rate for grasses or forbs. These results suggest that glyphosate crosses a competitive release threshold above which additional herbicide intensity yields diminishing returns for native recruitment. Both rates were sufficient to improve grass establishment at two sites, but neither translated into dense native stands within the 3-year observation window. Once *A. cristatum* was sufficiently reduced, the primary constraint on establishment shifted

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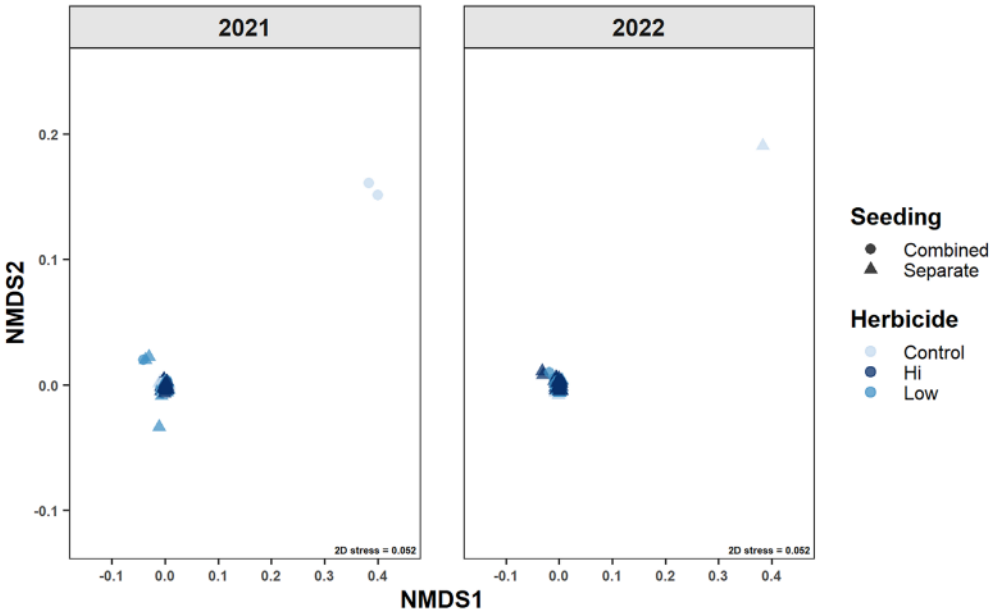


Figure 7. Two-dimensional NMDS ordination of background species community composition at Pine Butte Preserve (PBP; stress = 0.052). Points represent individual quadrat scores; herbicide treatment is indicated by color and seeding method by shape. Confidence ellipses are omitted; the sparse point distribution reflects low background species richness at this site. Herbicide-treated plots cluster near the origin in both years, distinct from control plots, consistent with strong suppression of background species following glyphosate application.

from competitive suppression to recruitment limitation. When competitive suppression is achieved, the next filter on native recovery operates at the level of the seedling microsite. Soil legacy effects and site-specific moisture deficits constrain safe site availability for germination and early survival, leaving native recruitment limited regardless of herbicide rate (Lesica & DeLuca 1996; Chambers 2000). Exceeding a suppression threshold matters more than maximizing herbicide rate. Where abiotic conditions are unfavorable, strong suppression alone will not produce native recovery. Additional site preparation or repeated interventions will be needed to overcome persistent establishment barriers.

Forb establishment was more constrained than grass establishment at every site. The divergence between grasses and forbs reflects differential sensitivity to the ecological filters operating below the competitive hierarchy. Grasses capitalize on competitive release more readily because their larger seeds and faster emergence rates provide a buffer against filter pressure during the critical recruitment window (Shackelford et al. 2021). Forbs require more precise alignment of microsite conditions and moisture availability to establish, making them disproportionately sensitive to the same filters (Young et al. 2017; Funk 2021; Jefferson et al. 2021). Where suppression created competitive release, initial forb gains were modest and did not persist, consistent with a closing resource pulse rather than a durable shift in recruitment conditions. Resource pulses created by herbicide application open establishment windows, but those windows are narrow, and forb seedlings are more vulnerable than grasses to moisture deficits and early colonization by nonseeded species during the critical recruitment period (Davis et al. 2000). Improving forb establishment in *A. cristatum* systems will likely require interventions beyond suppression and seeding alone, including targeted seedbed preparation, adjusted seeding densities, and seeding timed to favorable moisture windows.

Seeding configuration had little influence on native establishment across sites and response variables. Herbicide intensity explained far more variation in grass density, forb density, and community composition than seeding method at every site, suggesting that the magnitude of competitive release was the dominant filter on early recruitment rather than the spatial arrangement of functional groups. Where separate seeding produced modest forb density advantages at Berry Farm in some herbicide-year combinations, those differences were small and inconsistent across time. Spatial segregation of grasses and forbs via perpendicular drill passes did not reduce early competitive interference, likely because priority effects operate at finer temporal and spatial scales than the drill pass spacing implemented here. Faster-establishing grasses retain a competitive advantage over forbs even when seeded in separate passes if germination timing and seedling resource capture overlap substantially (Fukami 2015). Although spatially structured seeding can enhance establishment under some conditions (Porensky et al. 2012; Pokorny et al. 2020), these results do not support adopting separate seeding as a general prescription for *A. cristatum* restoration, given the logistical and cost burden of multiple drill passes.

The community-level consequences of glyphosate application extended well beyond what functional group responses alone revealed. Herbicide intensity explained the largest share of community-level variation at all three sites, far exceeding

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the contributions of year and seeding configuration. Herbicide-treated plots also showed greater among-quadrat compositional variability than controls at all sites. When a dominant competitor is reduced, microsite heterogeneity and stochastic colonization processes become more influential in governing assembly, increasing the range of possible post-treatment trajectories (Chase 2003). The elevated compositional variability in herbicide-treated plots warrants some caution in attributing treatment-group separation entirely to directional community shifts. The consistency and magnitude of herbicide effects across all three sites nevertheless support interpreting the diverging trajectories as genuine rather than artifactual. These diverging trajectories suggest that herbicide application is initiating state transitions rather than simply reducing cover of a single species, a pattern consistent with threshold dynamics in invaded grasslands (Suding et al. 2004).

Successful suppression created a secondary problem. In herbicide-treated plots at NARC and Berry Farm, other species cover increased sharply in the early post-treatment years then declined or stabilized, consistent with a transient resource pulse in which suppression temporarily elevated community invasibility (Davis et al. 2000). The opened niche was not captured by the seeded natives. Post-disturbance environments selectively favor ruderal life history strategies that allow early-establishing species to exploit resource pulses before competitive dynamics reassert (Grime 1977). In contrast, seeded long-lived perennial natives require multiple growing seasons to progress from seedling to competitive adult and are mismatched to the timescale of the post-suppression colonization window (Bakker & Wilson 2003; James et al. 2011). Suppression shifts rather than eliminates invasion risk. Incorporating rapidly establishing native annual species into seed mixes may help close the colonization window by preempting ruderal colonizers during the critical post-suppression period while longer-lived perennials establish over subsequent years (Sheley & Krueger-Mangold 2003).

Abiotic context shaped establishment outcomes as strongly as herbicide treatment across sites. NARC and Berry Farm, which experienced more favorable moisture conditions during early post-treatment years, showed clearer gains in seeded grasses and modest forb establishment. At PBP, moisture deficits and soil legacy effects were sufficiently strong to limit native recruitment even after competitive pressure was removed, pointing to site resistance that operated independently of herbicide treatment. Interannual precipitation and its seasonal timing exert strong controls on seedling survival and recruitment in semiarid systems, and site-level variation in these factors likely explains much of the establishment heterogeneity observed across sites (Hardegree et al. 2018; Copeland et al. 2021). Restoration practitioners should therefore interpret single-site or single-year outcomes cautiously. Interventions that appear ineffective under unfavorable climatic conditions will likely perform differently when suppression and seeding coincide with adequate moisture for seedling establishment (Butterfield et al. 2017).

The data from this study capture the early stages of a long transition process. Communities in herbicide-treated plots diverged substantially from controls in composition, cover, and species trajectories across 3 years, but they did not converge on diverse native assemblages. This is the expected signature of a system crossing a resistance threshold without yet reaching a new stable state. Increased variability and trajectory divergence precede any new equilibrium (Suding & Hobbs 2009). *A. cristatum*-dominated grasslands accumulate soil legacy effects, depleted seed banks, and modified nutrient cycling over decades of dominance, and those legacies do not reset on the timescale of a single suppression event (Hobbs & Norton 1996; Suding et al. 2004). Restoring these systems requires sustained directional pressure across multiple intervention cycles. Suppression must be followed by seeding timed to favorable climatic conditions, and both must be followed by management responses that prevent opportunistic colonizers from foreclosing native recovery. The 3-year benchmark reported here demonstrates that intense herbicide application can initiate that trajectory. Whether that trajectory continues toward diverse native composition depends on how practitioners respond during the critical post-suppression window (Seastedt et al. 2008). These systems do not resist restoration at the point of suppression. They resist it in the years that follow, in the narrow, sequential windows where seeding, climate, and management must align to carry a community across the threshold it has only begun to cross. That crossing remains possible under sustained management. It may simply take longer than 3 years, and require more than a single well-executed treatment.

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Supporting Information

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

Table S1. Mean crested wheatgrass cover (%) and standard deviation at NARC, Berry Farm, and PBP prior to grazing and herbicide application.

Table S2. PLS seed values by species at NARC, Berry Farm, and PBP.

Table S3. Type III Wald χ^2 tests for generalized linear mixed-effects models (GLMMs) fitted for each response variable at each site.

Table S4. PERMANOVA results by term for plant community composition at NARC, Berry Farm, and Pine Butte Preserve.

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