

Studying long-term, large-scale grassland restoration outcomes to improve seeding methods and reveal knowledge gaps

Matthew J. Rinella^{1*}, Erin K. Espeland² and Bruce J. Moffatt³

¹Rangeland Ecology, USDA/ARS Fort Keogh Livestock and Range Research Laboratory, 243 Fort Keogh Rd, Miles City, MT 59301, USA; ²Pest Management Unit, USDA/ARS Northern Plains Agricultural Research Laboratory, Sidney, MT, USA; and ³Soil Science Department, Oregon State University, Corvallis, OR, USA

Summary

1. Studies are increasingly investigating effects of large-scale management activities on grassland restoration outcomes. These studies are providing useful comparisons among currently used management strategies, but not the novel strategies needed to rapidly improve restoration efforts. Here we illustrate how managing restoration projects adaptively can allow promising management innovations to be identified and tested.

2. We studied 327 Great Plains fields seeded after coal mining. We modelled plant responses to management strategies to identify the most effective previously used strategies for constraining weeds and establishing desired plants. Then, we used the model to predict responses to new strategies our analysis identified as potentially more effective.

3. Where established, the weed crested wheatgrass (*Agropyron cristatum* L.) increased through time, indicating a need to manage establishment of this grass. Seeding particular grasses reduced annual weed cover, and because these grasses appeared to become similarly abundant whether sown at low or high rates, low rates could likely be safely used to reduce seeding costs. More importantly, lower than average grass seed rates increased cover of shrubs, the plants most difficult to restore to many grassland ecosystems. After identifying grass seed rates as a driver, we formulated model predictions for rates below the range managers typically use. These predictions require testing but indicated atypically low grass seed rates would further increase shrubs without hindering long-term grass stand development.

4. *Synthesis and applications.* Designing management around empirically based predictions is a logical next step towards improving ecological restoration efforts. Our predictions are that reducing grass seed rates to atypically low levels will boost shrubs without compromising grasses. Because these predictions derive from the fitted model, they represent quantitative hypotheses based on current understanding of the system. Generating data needed to test and update these hypotheses will require monitoring responses to shifts in management, specifically shifts to lower grass seed rates. A paucity of data for confronting hypotheses has been a major sticking point hindering adaptive management of most natural resources, but this need not be the case with degraded grasslands, because ongoing restoration efforts around the globe are providing continuous opportunities to monitor and manage processes regulating grassland restoration outcomes.

Key-words: adaptive management, *Agropyron cristatum*, *Bromus tectorum*, compositional data analysis, crested wheatgrass, Great Plains, rangeland, reclamation, seed rate, shrubs

Introduction

Many of the world's grasslands have become extensively degraded (Knapp 1996; Merritt & Dixon 2011), and the need to restore them has become widely recognized

*Correspondence author. E-mail: Matt.Rinella@ars.usda.gov
This article has been contributed to by US Government employees and their work is in the public domain in the USA.

(Millennium Ecosystem Assessment 2005). Grassland restoration efforts typically revolve around trying to reintroduce native species from seed, but seeding efforts often fail (e.g. Wilson *et al.* 2004; Rinella *et al.* 2012; Pyke, Wirth & Beyers 2013), and research is continuously devoted to improving these efforts. In recent years, a growing number of studies have investigated real-world restoration projects in order to better quantify long-term plant community responses to seeding and associated large-scale management activities. These studies of restoration in practice have yielded a variety of useful insights. For example, in rangelands, data gathered 1–30 years after land managers seeded extensive burned areas indicated seeding was most beneficial in areas uninvaded prior to fire, and dormant drill seeding without grazing provided better grass establishment than other treatments (Eiswerth & Shonkwiler 2006; Eiswerth *et al.* 2009; Knutson *et al.* 2014). Additionally, in abandoned cropland, data gathered 1–30 years after seeding identified the seed mix most rapidly generating reference conditions (Munson & Lauenroth 2012, 2014; Prach *et al.* 2014). Also, on German mine lands, data gathered 1–11 years after seeding quantified benefits of seeding over spontaneous regeneration (Tischew *et al.* 2014).

Studies of restoration in practice have provided useful comparisons among previously used management strategies but have not evaluated the novel strategies needed to quickly advance restoration management. The studies have been restricted to exploring factor managers previously chose/allowed to vary across locations, and the ranges of explored variation have reflected the typically narrow, risk-averse bounds of management. Also, because a number of potentially important factors have usually gone unknown or uncontrolled for (e.g. environmental conditions, seeded species genetics, seeding depth), findings from real-world restoration studies have been more provisional than findings from controlled experiments (Eiswerth & Shonkwiler 2006).

This paper illustrates how merging studies of restoration in practice with concepts from adaptive management could advance real-world restoration studies beyond their current role of comparing previously used management alternatives into the realm of discovering, robustly testing and refining novel strategies (Holling 1978; Walters & Hilborn 1978). We studied Great Plains grasslands that were seeded following coal mining disturbances. These grasslands are well suited for study, because the mines have been required to keep records on restoration activities for ~50 years, and during that time, seeding practices have varied widely within and among mines. The first priority for these grasslands is shifting compositions away from undesirable exotic species towards seeded grasses, forbs and shrubs. The second priority is boosting shrubs relative to grasses: shrubs are the plants most difficult to restore to Great Plains grasslands, as well as certain other expansive grassland systems (Bailey *et al.* 2010; Fansler & Mangold 2011).

As is generally done in real-world restoration studies, we began by modelling plant responses to environmental and management predictors in order to gain insights about previously used management strategies. Then, we took the additional step of using the model to pinpoint and predict responses to potentially effective management innovations. The model predictions represent quantitative, empirically based hypotheses amenable to testing and updating via Bayesian adaptive management. Compared to the intrinsically data-poor cases where adaptive management is usually attempted, prospects for learning while managing are enviable with grasslands. After being impacted by wildfires (e.g. Davies & Johnson 2011), mining (e.g. Booth *et al.* 1999), cropland conversion (e.g. Torok *et al.* 2010) or other disturbances, clusters of grassland sites are usually seeded over short time intervals. This opens possibilities for testing multiple management alternatives simultaneously, thereby avoiding the confounding of management and environmental effects that often occurs in adaptive management programs where management strategies (e.g. fish and game harvests, watershed flows) must be evaluated one at a time (Walters & Holling 1990; Sedinger & Herzog 2012; Biddle & Koontz 2014).

Materials and methods

RESTORATION PROCEDURES

Our study occurred on nine mines with mean annual precipitation, temperatures and growing season lengths of about 340 mm, 7 °C and 110 days, respectively (Fig. 1). We studied 327 fields on the mines, with fields being contiguous areas uniformly treated with one set of restoration inputs (e.g. seed rates, tillage). Prior to seeding, crushed rock extracted during mining was deposited to reconstruct pre-mining topography. Then, topsoil from large, long-term storage piles or directly from undisturbed grasslands about to be mined was spread over the rock (Fig. 2d). Soils of most fields (57%) were clay loams, though some fields had loams (20%), fine sandy clay loams (16%), clays (5%) and loamy sands

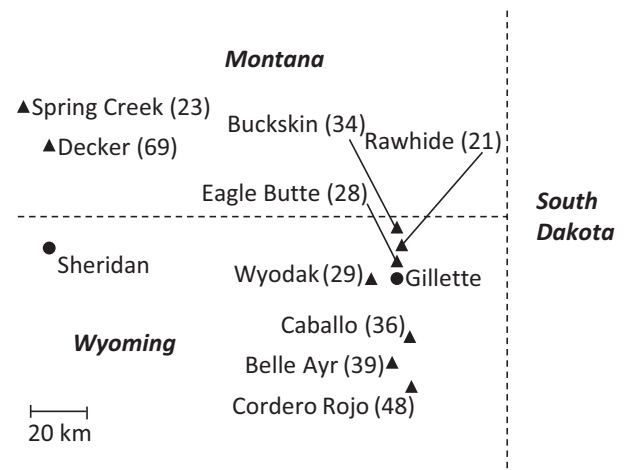


Fig. 1. Locations of coal mines (triangles) that participated in a grassland restoration study along with nearby cities (circles). Numbers indicate fields studied at each mine.

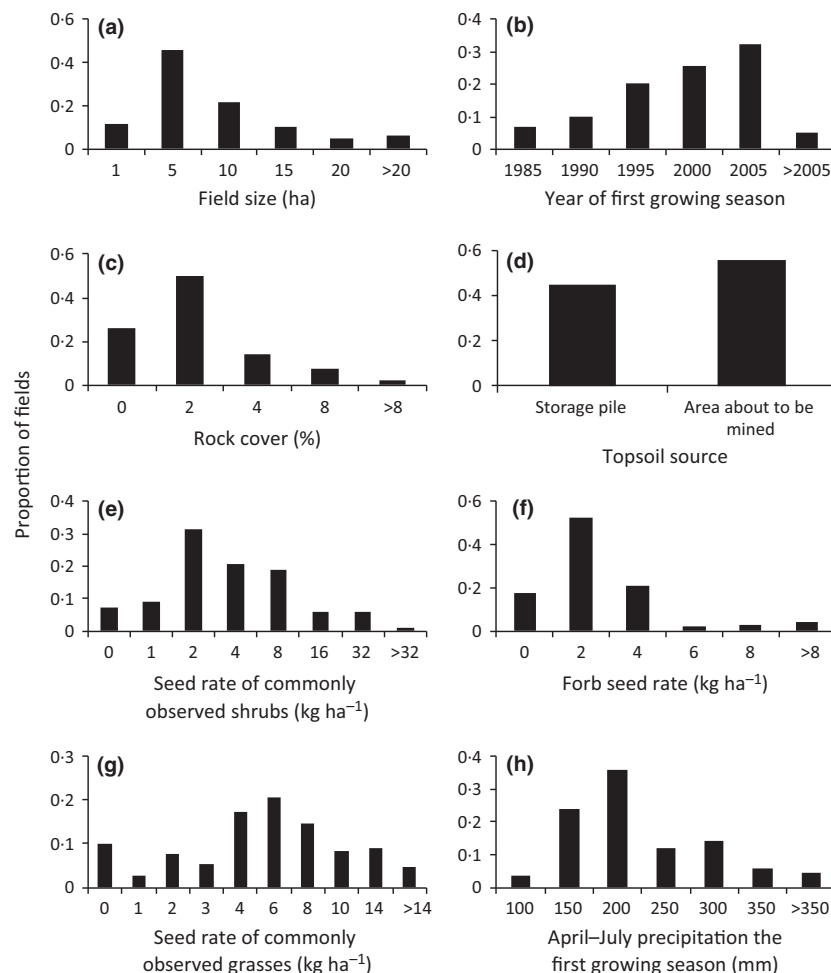


Fig. 2. Histograms depicting characteristics of grassland fields subjected to restoration treatments following mining. Panel (a) describes field sizes and panels (b–h) describe predictors in a model used to analyse vegetation compositions on the fields.

(2%). Generally within a year of spreading topsoil, fields were tilled then drilled and/or broadcasted with mixes of 14.8 ± 5.5 species (mean \pm SD). Species were perennial grasses, forbs and shrubs sown at 13.8 ± 6.8 , 1.6 ± 2.1 and 5.5 ± 7.7 , kg ha^{-1} , respectively, where all rates are of pure live seed (Table 1). Additionally, cereal grass nurse crops were sown in 32% of fields and non-native perennial forbs were sown in 43% of fields, but these species were rarely encountered during sampling. Seeded grasses were predominately native, but non-native perennials intermediate wheatgrass (*Thinopyrum intermedium* (Host) Barkworth & D.R. Dewey), reed canarygrass (*Phalaris arundinacea* L.), pubescent wheatgrass (*Agropyron trichophorum* (Link) Richter), Kentucky bluegrass (*Poa pratensis* L.), Canada bluegrass (*Poa compressa* L.) and/or sheep fescue (*Festuca ovina* L.) were seeded in 15% of fields.

VEGETATION MEASUREMENT

Fields were sampled 14 ± 6 years after seeding (Fig. 2b). Because plant production can vary widely by year, we sampled 2 years. About 50% of fields were sampled both years, 2011 and 2012, while remaining fields were sampled either 2011 (82 fields) or 2012 (81 fields). Sampling occurred 22 June 2011 to 9 August 2011 and 30 May 2012 to 16 August 2012, with each years' sampling of a mine occurring over <10 days.

Surface cover of rocks and the plant groups native perennial grasses, exotic perennial grasses, native perennial forbs, exotic

perennial forbs, exotic annual grasses, exotic annual forbs and native shrubs was visually estimated in 20 frames (20×50 cm) evenly spaced along each field's longest possible transect. For two mines, Decker and Spring Creek (Fig. 1), we included shrub data from a concurrent study (Rinella *et al.* 2015). Here, shrub cover was measured in 1–3 (depending on field size) 4.6×45.7 -m areas occurring at even intervals along each field's longest transect. These larger areas were better suited for quantifying sparsely distributed shrubs. Shrub cover values analysed in this study were area-weighted means of the two studies.

ANALYSIS

For analytical details, see Appendix S1 (Supporting information). Our response variables were cover of (i) seeded exotic and native perennial grasses (hereafter seeded grasses), (ii) unseeded exotic perennial grasses (hereafter exotic perennial grasses), (iii) exotic annual grasses and annual and biennial forbs (hereafter annual weeds), (iv) native forbs and (v) native shrubs. For each field, mean cover of each plant group was divided by mean total cover (See eqn S1 of Appendix S1). This conversion to 'relative cover' helped control for unmeasured variables (see Appendix S1). Relative cover values sum to 1.0, and transformations are necessary to accommodate this constraint (Aitchison 1986). We used a transformation that generates log ratios of plant cover values, such as $\log(\text{shrub cover}/\text{seeded grass cover})$.

Table 1. Native species sown during efforts to restore grassland fields following intense disturbance

	Scientific names	% of fields sown
<i>Grasses</i>		
*western wheatgrass	<i>Pascopyrum smithii</i> (Rydb.) Á. Löve	87
*green needlegrass	<i>Stipa viridula</i> Trin.	83
blue grama	<i>Bouteloua gracilis</i> (Kunth) Lag. ex Steud.	74
bluebunch wheatgrass	<i>Elytrigia spicata</i> (Pursh) D.R. Dewey	58
*slender wheatgrass	<i>Elymus trachycaulus</i> (Link) Gould ex Shinners	55
*thickspike wheatgrass	<i>Elymus lanceolatus</i> (Scribn. & J.G. Smith) Gould	55
little bluestem	<i>Schizachyrium scoparium</i> (Michx.) Nash	44
Indian ricegrass	<i>Oryzopsis hymenoides</i> (Roem. & Schult.) Ricker	40
prairie junegrass	<i>Koeleria macrantha</i> (Ledeb.) Schult.	37
sideoats grama	<i>Bouteloua curtipendula</i> (Michx.) Torr.	34
needleandthread	<i>Hesperostipa comata</i> (Trin. & Rupr.) Barkworth	29
1 additional species		29
≥2 additional species		31
<i>Forbs</i>		
*western yarrow	<i>Achillea millefolium</i> L. var. <i>occidentalis</i> DC.	65
*purple prairie clover	<i>Dalea purpurea</i> Vent. var. <i>purpurea</i>	50
*prairie coneflower	<i>Ratibida columnifera</i> (Nutt.) Woot. & Standl.	41
*milkvetch	<i>Astragalus canadensis</i> L.	32
scarlet globemallow	<i>Sphaeralcea coccinea</i> (Nutt.) Rydb.	17
lupine	<i>Lupinus</i> spp.	15
*white prairie clover	<i>Dalea candida</i> Michx. ex Willd.	9
Lewis flax	<i>Linum lewisii</i> Pursh	8
purple prairie coneflower	<i>Echinacea angustifolia</i> DC.	8
1 additional species		7
≥2 additional species		15
<i>Shrub</i>		
*big sagebrush	<i>Artemisia tridentata</i> Nutt.	68
*fourwing saltbush	<i>Atriplex canescens</i> (Pursh) Nutt.	67
*winterfat	<i>Krascheninnikovia lanata</i> (Pursh) A. Meeuse & Smit	66
*fringed sage	<i>Artemisia frigida</i> Willd.	32
*rubber rabbitbrush	<i>Ericameria nauseosa</i> (Pall. ex Pursh) G.L. Nesom & Baird	31
silver sagebrush	<i>Artemisia cana</i> Pursh	28
*Gardner's saltbush	<i>Atriplex lentiformis</i> (Torr.) S. Watson	17
skunkbush sumac	<i>Rhus trilobata</i> Nutt.	10
Woods' Rose	<i>Rosa woodsii</i> Lindl.	9
shadscale saltbush	<i>Atriplex confertifolia</i> (Torr. & Frém.) S. Watson	4
prairie rose	<i>Rosa arkansana</i> Porter	4
1 additional species		13
≥2 additional species		5

Asterisks denote species commonly observed in the fields, and seed rates of these species served as predictors in a model used to explain vegetation abundances on the fields.

We fit a multivariate linear model to the transformed data averaged across sampling years (see Appendix S1). The model had terms indicating whether fields were sampled 2011, 2012 or both years, as well as terms for mine, mine × years since seeding and the two different sampling area sizes. Precipitation the first growing season (i.e. April 1–July 31) following seeding was included as a predictor because this precipitation period influences plant survival in the region (Bakker *et al.* 2003). Precipitation data came from nearest National Oceanic and Atmospheric Administration weather stations (<http://www.noaa.gov/>). Four categorical grass seed rate predictors were included: (i) 0–0, (ii) >0–0 to ≤4–0, (iii) <4–0 to ≤8–0, and (iv) >8–0 kg ha⁻¹. These ranges are sums of native and non-native rates, excluding natives rarely/never observed during sampling (Table 1). Because the rate variable excluding rarely observed grasses was correlated

with the total grass rate variable, analyses based on either variable gave roughly similar estimates, but excluding rarely observed grasses prevented the misleading conclusion that species incapable of establishing have strong effects. The grass seed rate boundary choices, which provided large sample sizes for each category (Fig. 2g), were informed by a previous study conducted at one of our study mines (fig. 3 of Williams *et al.* 2002; fig. 3 of Hild *et al.* 2006). Forb seed rate was a continuous predictor (Fig. 2f), as was shrub seed rate (Fig. 2e), excluding shrubs rarely/never observed during sampling (Table 1). A categorical predictor indicated whether topsoil was directly re-deposited or stored (Fig. 2d). Rock cover (Fig. 2c) was a predictor for Spring Creek and Decker, the only mines where rock cover exceeded low values. We based inferences on 95% Bayesian confidence intervals (CI), and probabilities effects were positive or negative (Pr).

Results

Annual weeds were abundant (Fig. 3), with cover nearly evenly split between annual grasses [i.e. cheatgrass and Japanese brome (*Bromus arvensis* L.)] and forbs [yellow sweetclover (*Melilotus officinalis* (L.) Lam.), common lambsquarters (*Chenopodium album* L.) and mustards (Brassicaceae spp.)]. Among the region's common native grasses, western wheatgrass, thickspike wheatgrass, slender wheatgrass and green needlegrass appeared somewhat uniquely capable of reducing annual weeds (Table 1, Fig. 4a). Where these grasses were sown at low rates (i.e. >0.0 to 4.0 kg ha⁻¹), the annual weed to seeded grass cover ratio averaged 1.5(0.7, 3.3) [point estimate (95% CI)], compared to 2.8(1.1, 6.7) where these grasses were not sown. This difference was significant with probability 0.98 (Pr = 0.98). There was little evidence increasing grass seed rates above the low range further suppressed annual weeds (Fig. 4a). Time since seeding, topsoil handling, rocks and first growing season precipitation did not measurably impact annual weed cover ratios (Fig. 4a).

Unlike annual weeds, shrubs were not detectably suppressed by the low grass seed rate range (i.e. >0.0 to 4.0 kg ha⁻¹; Fig. 4b). Also unlike annual weeds, shrubs became increasingly suppressed with increasing grass seed rates (compare Fig. 4a,b). On average, the shrub to seeded grass cover ratio was 0.10(0.02, 0.53), 0.10(0.03, 0.41), 0.02(0.007, 0.09) and 0.009(0.002, 0.04) when commonly observed grasses were seeded at 0.0, >0.0 to 4.0, >4.0 to 8.0 and >8.0 kg ha⁻¹, respectively. The shrub to seeded grass cover ratio increased 13%(1%, 40%) with every 1.0 SD (i.e. 6.7 kg ha⁻¹) increase in shrub seed rate. There was weak evidence direct topsoil relocation, rocks and low precipitation the first growing season benefited shrubs (Fig. 4b). Forbs were not measurably affected by factors explored in this study (data not shown).

Crested wheatgrass and smooth brome (*Bromus inermis* Leyss.) were the only unseeded exotic perennial grasses

observed, with the latter rarely observed. Cover of these grasses varied widely among fields (Fig. 3). None of the grass seed rates ranges measurably impacted unseeded exotic perennial grasses cover ratios (Fig. 4c). Compared to storing topsoil, directly relocating topsoil favoured unseeded exotic perennial grasses (Pr = 0.98), and low rock cover also favoured these grasses (Pr > 0.99; Fig. 4c). Exotic perennial grass cover ratios were greater on older fields (Pr > 0.99; Fig. 4c).

Except for exotic perennial grasses, vegetation responses varied appreciably among mines, even after controlling for factors in the model (Fig. 5). For example, the Spring Creek annual weed point estimate of -1.3 indicates this mine's mean annual weed value was only $100 \times e^{-1.3} = 27\%$ of the average mine value, while the Buckskin point estimate of 0.8 indicates this mine's annual weed value was $100 \times (e^{0.8} - 1.0) = 123\%$ greater than the average mine value (Fig. 5e). To illustrate how mine-to-mine variability affects model predictions, we predicted shrub to grass cover ratios resulting from two seed rate treatments (Fig. 6). We made the predictions for two studied mines (i.e. Caballo and Spring Creek) as well as all regional mines we did not study (Fig. 6). Deriving predictions for unstudied mines required integrating over the population distribution of mine effects (see Appendix S1 MODEL PREDICTIONS section). Predictions are equivalent for all unstudied mines, due to the absence of data on these mines. Prediction uncertainty is considerably greater (i.e. confidence intervals wider) for unstudied than studied mines (Fig. 6), and this owes to the extensive shrub cover variation among studied mines (Fig. 5d). If mine-to-mine variation was smaller, unstudied mine prediction accuracy would be greater.

Predicted cover ratio differences (i.e. Fig. 6, circles minus diamonds) are equivalent for all mines on the log scale (i.e. proportionally), but this is not so on the untransformed scale: point estimates indicate predicted shrub to grass cover ratios for low and high grass seed

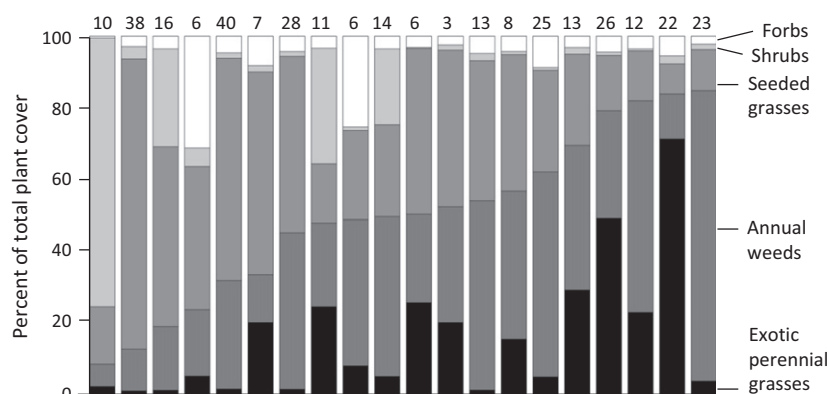


Fig. 3. Relative cover of plant groups on grasslands that received restoration treatments following mining. Values above bars are numbers of fields with corresponding compositions. For example, the furthest right bar indicates 23 fields had roughly 4, 81, 11, 1 and 2 per cent cover of the five plant groups. Fields were grouped into clusters based on Euclidian distances, and graphed values represent cluster means.

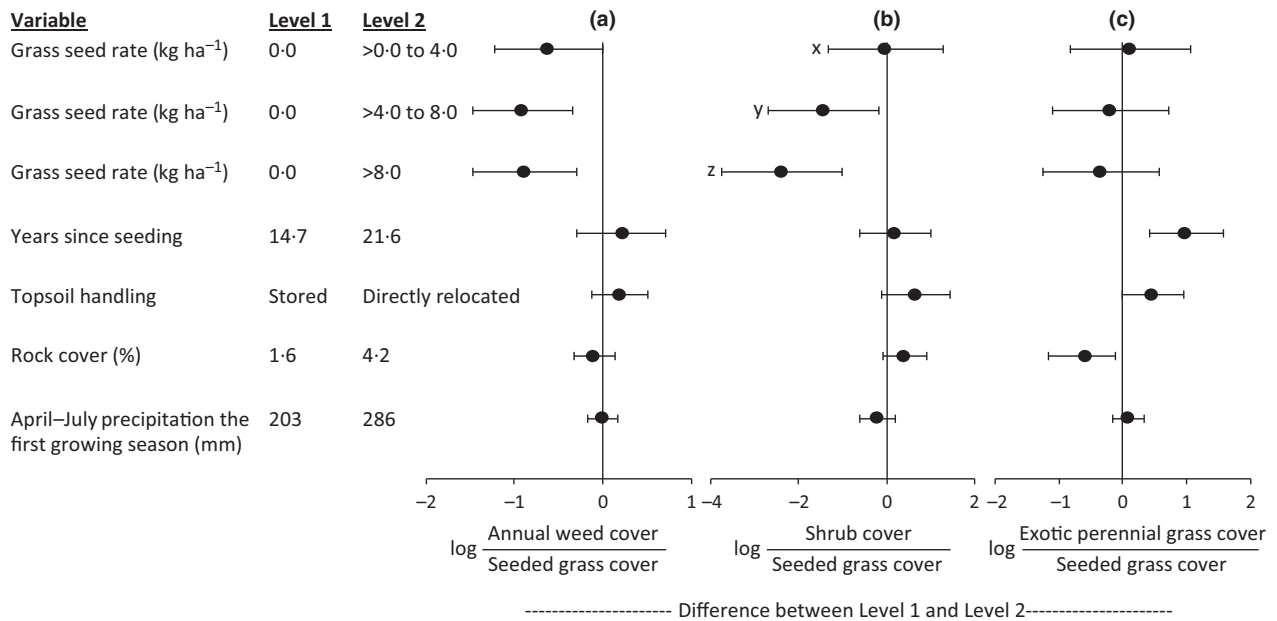


Fig. 4. Point estimates (dots) and 95% CIs (bars) quantifying differences between Level 1 and 2 treatments. For example, the negative CI in the second row of panel (a) indicates that, compared to the 0.0 rate, rates in the range >4.0 to 8.0 kg ha⁻¹ reduced annual weed to seeded grass cover ratios. Because this CI does not overlap zero, the probability of this annual weed reduction exceeds 0.975 (Pr > 0.975). Grass seed rate ranges exclude species rarely/never observed on the mines. The x, y and z of panel (b) indicate shrub to seeded grass ratios differed (Pr > 0.95) among corresponding Level 2 grass seed rate ranges. Restoration began with topsoil placement, and the topsoil CIs suggest shrub to seeded grass ratios (panel b) and exotic perennial grass to seeded grass ratios (panel c) were greater where topsoil came from areas about to be mined compared to large storage piles. Level 1 and 2 values for years since seeding, rock cover and precipitation represent means and means + 1 SD, respectively.

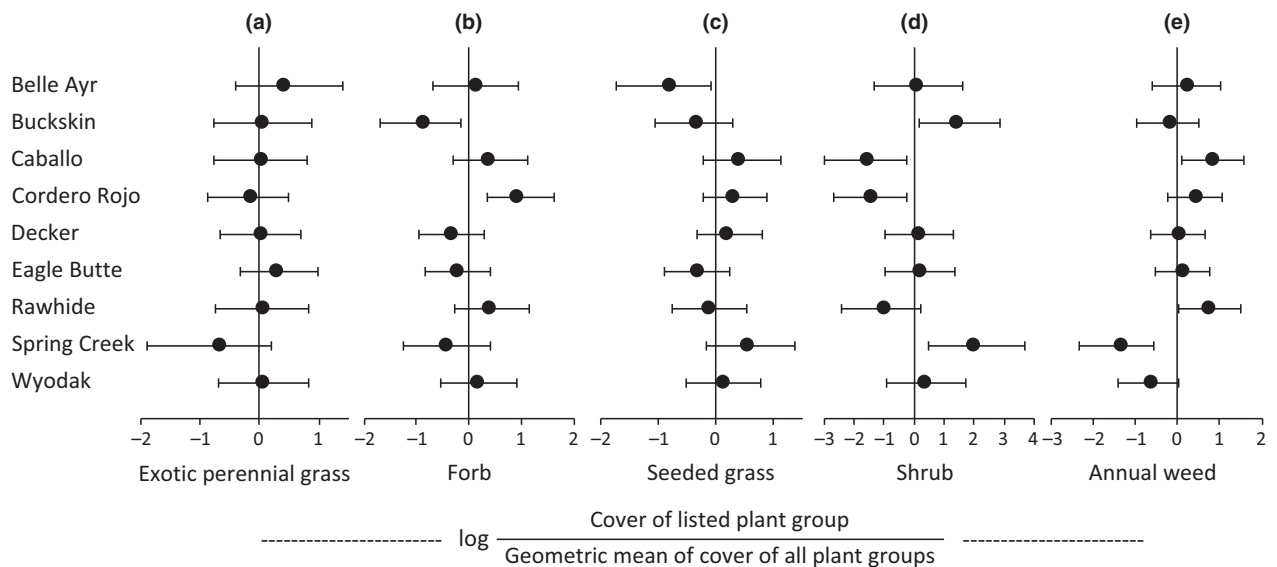


Fig. 5. Point estimates (dots) and 95% CIs (bars) describing mine effects; that is plant cover differences remaining after controlling for management, environmental and other predictors (e.g. seed rate, precipitation, time since seeding). Units of panels (a–e) reflect centred log-ratio transformation. Negative and positive mine effects, respectively, indicate cover ratios lower and higher than the average across mines. CIs not overlapping zero indicate mines with a >0.975 probability of differing from the average across mines.

rates, respectively, are $e^{-0.7} = 0.5$ and $e^{-2.3} = 0.1$ at Spring Creek versus $e^{-4.1} = 0.02$ and $e^{-5.7} = 0.003$ at Caballo (Fig. 6). The larger difference for Spring Creek is because of this mine's relatively large mean shrub cover (Fig. 5d).

Discussion

INSIGHTS FROM PAST MANAGEMENT

Fields sown with certain grass species, either singly or in combination, had substantially lower relative annual

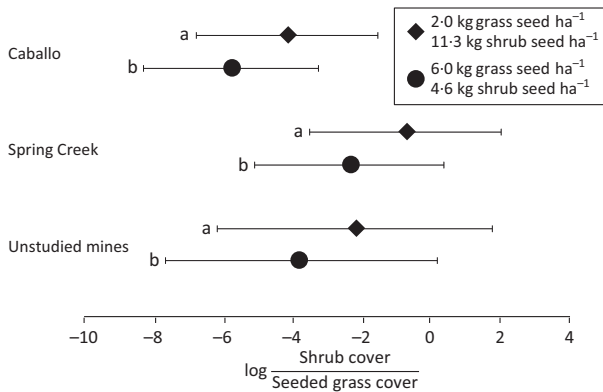


Fig. 6. Point estimates (dots) and 95% CIs (bars) summarizing model predictions of cover ratios on fields subjected to future mining then seeding. Predictions are for mines where previously seeded fields have relatively low (Caballo) and high (Spring Creek) shrub abundances as well as regional mines omitted from our study (unstudied mines). Different letters within mines indicate significant predicted differences ($P > 0.99$).

weed cover (Table 1, Fig. 4a). The same grasses that constrained annual weeds constrained shrubs, but only when sown at high rates (Fig. 4b). Low grass seed rates likely provided large interplant spaces where shrubs could establish before the onset of intense grass competition (Table 1, Fig. 4b). Shrubs are thought to coexist with grasses by exploiting deeper soil layers (Ward, Wiegand & Getzin 2013; Cipriotti *et al.* 2014), and low grass rates presumably allowed shrubs to penetrate deep layers before grass competition intensified (Brown & Archer 1990; Kambatuku, Cramer & Ward 2013). Delaying onset of grass competition has aided shrubs in other studies (Blaisdell 1949; Hubbard 1957; Porensky *et al.* 2014), including one conducted at our Belle Ayr mine (Williams *et al.* 2002; Hild *et al.* 2006) and another at our Decker and Spring Creek mines (Rinella *et al.* 2015). Rinella *et al.* (2015) also concluded high establishment year precipitation reduced shrubs, presumably by accelerating onset of grass competition, a finding mirrored by other studies (Doerr, Redente & Sievers 1983; Soliveres, Monerri & Cortina 2012). Evidence for a negative precipitation effect was weaker in the current study (i.e. $P = 0.85$; Fig. 4b), which is unsurprising given the Rinella *et al.* (2015) analysis was more detailed with respect to shrubs.

We observed no effect of grass seeding rates on forbs (data not shown). More generally, besides displaying some variability among mines (Fig. 5b), forbs were not measurably influenced by any of the studied variables. Relative forb abundances on the mines were not unlike those typically observed on natural northern Great Plains grasslands (Fig. 3; Samuel & Hart 1998; Vermeire, Heitschmidt & Rinella 2009), suggesting a wide range of practices can restore forbs to natural levels.

A potential risk in reducing grass seeding rates to aid shrubs is this might result in sparse grass stands that

inadequately suppress annual weeds. However, features of our data suggest this risk is minimal. When measured long after seeding, annual weed to seeded grass cover ratios did not vary significantly with grass seed rates (Fig. 4a), seeding methods (see Appendix S1) and first growing season precipitation (Fig. 4a), factors routinely influencing seeded grass abundances shortly after seeding (e.g. Bakker *et al.* 2003; Mangold, Poulsen & Carpinelli 2007; Hulvey & Aigner 2014; Schantz, Sheley & James 2015). The lack of measurable long-term effects of these factors likely reflects seeded grasses increasing when rare until becoming limited by competitive feedbacks (Weiner & Freckleton 2010). A seed rate study at our Belle Ayr mine found grass biomass increased with western, thick-spike and slender wheatgrass seed rate 2 but not ≥ 3 years post-seeding (Williams *et al.* 2002; Hild *et al.* 2006), directly indicating grasses of our study can increase to carrying capacity in the system (Table 1). Additionally, long-term monitoring at our Decker mine revealed initially small western wheatgrass populations can gradually increase in annual weed-dominated fields (Producers 2013).

Exotic perennial grasses, particularly crested wheatgrass, are a major obstacle to achieving restoration goals in our system (Fig. 3) and others (e.g. Davies, Boyd & Nafus 2013). Older fields supported more crested wheatgrass (Fig. 4c), implying that over time, either crested wheatgrass populations grew or reclamation procedures improved (e.g. less seed source contamination). To determine which of these possibilities is more plausible, we combined our data with older monitoring data on the same fields gathered by mine personnel (see Appendix S1 LONGITUDINAL MODEL section). This longitudinal data set revealed that, once established, crested wheatgrass populations can gradually increase and out-compete seeded species (Fig. S1), thus indicating the importance of preventing crested wheatgrass establishment. The combined data set also revealed crested wheatgrass tends to establish around the time of seeding: in fields where crested wheatgrass was not detected early (≤ 3 years post-seeding), the chance it would be detected later (> 3 years post-seeding) was only 19%, compared to a 77% chance of later detection where it was detected early. Efforts to prevent crested wheatgrass establishment are most important around the time of seeding, when seeded species remain small/uncompetitive and crested wheatgrass seed influxes are most likely. Crested wheatgrass often occurs on soon-to-be mined sites, and directly relocating topsoil from these sites, as opposed to first storing it in large, deep piles, appears to encourage crested wheatgrass by re-depositing its short-lived seeds and/or root fragments near the soil surface (James, Svejcar & Rinella 2011; Fig. 4c). Other strategies for preventing crested wheatgrass establishment might involve controlling this species prior to transporting soils or adopting more stringent seed purity standards.

ADAPTIVE MANAGEMENT

Because our model is Bayesian, its predictions, or equivalently hypotheses, are probability distributions, which we summarize by modes and 95% CIs (Fig. 6). Gathering data that bear on the model's predictions would increase knowledge of the system and allow for Bayesian adaptive management (e.g. Moore & McCarthy 2010; Rumpff *et al.* 2011; Fukasawa *et al.* 2013). For instance, the Fig. 6 seed rate combination predicted to favour shrubs could be used on some number of fields, and resulting vegetation could be measured after several years. This would allow updating of the Fig. 6 hypotheses, which in practice would entail combining the old and new data and refitting the model. The updated probability distributions/hypotheses would represent compromises between old and new data. If, for example, the mean of the new data exceeded point estimates of Fig. 6, the updated 95% CIs would be shifted to larger values, with the magnitudes of the shifts and the width of the CIs depending on the new data variance and sample size. The updated hypotheses might motivate modest adjustments in future rounds of management. For example, if the updated hypotheses indicated the low grass seed rate of Fig. 6 benefited shrubs while minimally affecting seeded grasses, this might inspire a further rate reduction, and monitoring responses to this even lower rate would allow further hypothesis updating.

The iterative approach just described is termed 'passive' adaptive management (Walters 1986). In passive adaptive management, the overriding objective is managing as effectively as possible given the current state of knowledge, and gaining knowledge to improve future management is a secondary objective attained through monitoring responses to slowly evolving practices. This contrasts with 'active' adaptive management, where rapid knowledge gains are more highly prioritized, so somewhat non-standard practices are used in a manner that fosters learning (Walters 1986). An intuitive active adaptive management step for the region's mines would entail refining our model's most tenuous hypotheses. For example, our data set is compatible with the hypothesis that grass seed rates between >0.0 and 4.0 kg ha^{-1} give equivalent vegetation responses, but this compatibility does not mean the hypothesis is true, or even that it is necessarily close enough to true for management purposes. Comparing rarely used low rates (e.g. $0.01\text{--}1.0 \text{ kg ha}^{-1}$) to more typical rates (e.g. $>1.0\text{--}4.0 \text{ kg ha}^{-1}$) in a replicated scheme holding important factors (e.g. seeding year, mine) constant might reveal additional predictors needed to model subdivisions of this range (e.g. <0.1 , $0.1\text{--}1.0$, $>1.0\text{--}4.0 \text{ kg ha}^{-1}$). Active adaptive management is often advocated as a means for addressing 'structural uncertainty', which can be thought of as uncertainty about the need for additional predictors (Walters & Holling 1990; Gregory, Ohlson & Arvai 2006). Restoration managers and researchers collaborating to determine which model-based

hypotheses to refine may help groups reach consensus about explicit areas where understanding is lacking and needed (Walters & Holling 1990; Failing, Gregory & Higgins 2013).

Adaptive management has proven conceptually appealing in the decades since being formally described (Holling 1978; Walters & Hilborn 1978), and it has been adopted in limited contexts (Bryan *et al.* 2009; Mackenzie & Keith 2009; Jones, Brenden & Irwin 2015), but there are notable barriers to widespread adoption (e.g. Moir & Block 2001; Allan & Curtis 2005), and the vast majority of natural resources remain non-adaptively managed. However, some of the barriers plaguing adoption in other systems should not impede adoption in grassland restoration. In ours' and a variety of other grassland restoration efforts, multiple areas are often seeded within individual years (e.g. Knutson *et al.* 2014; Grman *et al.* 2015), thereby avoiding the confounding of environmental and management effects that occurs when only one observation of the response(s) is realized each monitoring period (Walters & Holling 1990; Sedinger & Herzog 2012; Biddle & Koontz 2014). Also, compared to many adaptive management programs [e.g. endangered species programs (Runge 2011; Hartmann *et al.* 2015)], risks of experimental practices are milder in grasslands because fields can be, and in our system often are, reseeded when initial seeding fails.

Studies of grassland restoration in practice are steadily proliferating throughout much of the World (Deri *et al.* 2011; Desserud & Naeth 2014; Munson & Lauenroth 2014; Tischew *et al.* 2014; Gilhaus, Vogt & Holzel 2015; Prach *et al.* 2015). A major goal of these studies is comparing the effectiveness of management alternatives, comparisons only possible because managers have chosen to experiment with different practices in different areas under their care. Experimentation is a critical component of adaptive management, so the widespread willingness to experiment is a positive sign successful adaptive management programs could be devised for grassland systems. Using the methods we describe here to expand studies of restoration in practice into adaptive management programs is a logical next move towards reversing degradation of the world's grassland ecosystems.

Data accessibility

Data on management and environmental variables and plant responses are available from Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.k5st3> (Rinella, Espeland & Moffatt 2016).

References

- Aitchison, J. (1986) *The Statistical Analysis of Compositional Data: Monographs on Statistics and Applied Probability*. Chapman & Hall Ltd., London.
- Allan, C. & Curtis, A. (2005) Nipped in the bud: why regional scale adaptive management is not blooming. *Environmental Management*, **36**, 414–425.
- Bailey, D.W., Al Tabini, R., Waldron, B.L., Libbin, J.D., Al-Khalidi, K., Alqadi, A., Al Oun, M. & Jensen, K.B. (2010) Potential of *Kochia*

- prostrata and perennial grasses for rangeland restoration in Jordan. *Rangeland Ecology & Management*, **63**, 707–711.
- Bakker, J.D., Wilson, S.D., Christian, J.M., Li, X.D., Ambrose, L.G. & Waddington, J. (2003) Contingency of grassland restoration on year, site, and competition from introduced grasses. *Ecological Applications*, **13**, 137–153.
- Biddle, J.C. & Koontz, T.M. (2014) Goal specificity: a proxy measure for improvements in environmental outcomes in collaborative governance. *Journal of Environmental Management*, **145**, 268–276.
- Blaisdell, J.P. (1949) Competition between sagebrush seedlings and reseeded grasses. *Ecology*, **30**, 512–519.
- Booth, D.T., Gores, J.K., Schuman, G.E. & Olson, R.A. (1999) Shrub densities on pre-1985 reclaimed mine lands in Wyoming. *Restoration Ecology*, **7**, 27–32.
- Brown, J.R. & Archer, S. (1990) Water relations of a perennial grass and seedling vs adult woody plants in a subtropical savanna, Texas. *Oikos*, **57**, 366–374.
- Bryan, B.A., Kandulu, J., Deere, D.A., White, M., Frizenschaf, J. & Crossman, N.D. (2009) Adaptive management for mitigating Cryptosporidium risk in source water: a case study in an agricultural catchment in South Australia. *Journal of Environmental Management*, **90**, 3122–3134.
- Cipriotti, P.A., Aguiar, M.R., Wiegand, T. & Paruelo, J.M. (2014) A complex network of interactions controls coexistence and relative abundances in Patagonian grass-shrub steppes. *Journal of Ecology*, **102**, 776–788.
- Davies, K.W., Boyd, C.S. & Nafus, A.M. (2013) Restoring the sagebrush component in crested wheatgrass-dominated communities. *Rangeland Ecology & Management*, **66**, 472–478.
- Davies, K.W. & Johnson, D.D. (2011) Are we “missing the boat” on preventing the spread of invasive plants in rangelands? *Invasive Plant Science and Management*, **4**, 166–172.
- Deri, E., Magura, T., Horvath, R., Kisfali, M., Ruff, G., Lengyel, S. & Tothmeresz, B. (2011) Measuring the short-term success of grassland restoration: the use of habitat affinity indices in ecological restoration. *Restoration Ecology*, **19**, 520–528.
- Desserud, P.A. & Naeth, M.A. (2014) Predicting grassland recovery with a state and transition model in a natural area, central Alberta, Canada. *Natural Areas Journal*, **34**, 429–442.
- Doerr, T.B., Redente, E.F. & Sievers, T.E. (1983) Effect of cultural practices on seeded plant communities on intensively disturbed soils. *Journal of Range Management*, **36**, 423–428.
- Eiswerth, M.E. & Shonkwiler, J.S. (2006) Examining post-wildfire reseeding on and rangeland: a multivariate tobit modelling approach. *Ecological Modelling*, **192**, 286–298.
- Eiswerth, M.E., Krauter, K., Swanson, S.R. & Zielinski, M. (2009) Post-fire seeding on Wyoming big sagebrush ecological sites: regression analyses of seeded nonnative and native species densities. *Journal of Environmental Management*, **90**, 1320–1325.
- Failling, L., Gregory, R. & Higgins, P. (2013) Science, uncertainty, and values in ecological restoration: a case study in structured decision-making and adaptive management. *Restoration Ecology*, **21**, 422–430.
- Fansler, V.A. & Mangold, J.M. (2011) Restoring native plants to crested wheatgrass stands. *Restoration Ecology*, **19**, 16–23.
- Fukasawa, K., Hashimoto, T., Tataru, M. & Abe, S. (2013) Reconstruction and prediction of invasive mongoose population dynamics from history of introduction and management: a Bayesian state-space modelling approach. *Journal of Applied Ecology*, **50**, 469–478.
- Gilhaus, K., Vogt, V. & Holzel, N. (2015) Restoration of sand grasslands by topsoil removal and self-greening. *Applied Vegetation Science*, **18**, 661–673.
- Gregory, R., Ohlson, D. & Arvai, J. (2006) Deconstructing adaptive management: criteria for applications to environmental management. *Ecological Applications*, **16**, 2411–2425.
- Grman, E., Bassett, T., Zirbel, C.R. & Brudvig, L.A. (2015) Dispersal and establishment filters influence the assembly of restored prairie plant communities. *Restoration Ecology*, **23**, 892–899.
- Hartmann, S.A., Segelbacher, G., Juina, M.E. & Schaefer, H.M. (2015) Effects of habitat management can vary over time during the recovery of an endangered bird species. *Biological Conservation*, **192**, 154–160.
- Hild, A.L., Schuman, G.E., Vicklund, L.E. & Williams, M.I. (2006) Canopy growth and density of Wyoming big sagebrush sown with cool-season perennial grasses. *Arid Land Research and Management*, **20**, 183–194.
- Holling, C.S. (1978) *Adaptive Environmental Assessment and Management*. John Wiley and Sons, New York, New York, USA.
- Hubbard, R.L. (1957) The effect of plant competition on the growth and survival of bitterbrush seedlings. *Journal of Range Management*, **10**, 135–137.
- Hulvey, K.B. & Aigner, P.A. (2014) Using filter-based community assembly models to improve restoration outcomes. *Journal of Applied Ecology*, **51**, 997–1005.
- James, J.J., Svejcar, T.J. & Rinella, M.J. (2011) Demographic processes limiting seedling recruitment in aridland restoration. *Journal of Applied Ecology*, **48**, 961–969.
- Jones, M.L., Brenden, T.O. & Irwin, B.J. (2015) Re-examination of sea lamprey control policies for the St. Marys River: completion of an adaptive management cycle. *Canadian Journal of Fisheries and Aquatic Sciences*, **72**, 1538–1551.
- Kambatuku, J.R., Cramer, M.D. & Ward, D. (2013) Overlap in soil water sources of savanna woody seedlings and grasses. *Ecohydrology*, **6**, 464–473.
- Knapp, P.A. (1996) Cheatgrass (*Bromus tectorum* L.) dominance in the Great Basin desert. *Global Environmental Change*, **6**, 37–52.
- Knutson, K.C., Pyke, D.A., Wirth, T.A., Arkle, R.S., Pilliod, D.S., Brooks, M.L., Chambers, J.C. & Grace, J.B. (2014) Long-term effects of seeding after wildfire on vegetation in Great Basin shrubland ecosystems. *Journal of Applied Ecology*, **51**, 1414–1424.
- Mackenzie, B.D.E. & Keith, D.A. (2009) Adaptive management in practice: conservation of a threatened plant population. *Management and Restoration*, **10**(s1), S129–S135.
- Mangold, J.M., Poulsen, C.L. & Carpinelli, M.F. (2007) Revegetating Russian knapweed (*Acroptilon repens*) infestations using morphologically diverse species and seedbed preparation. *Rangeland Ecology and Management*, **60**, 378–385.
- Menardo, F., Praz, C.R., Wyder, S., Ben-David, R., Bourras, S., Matsumae, H., *et al.* (2016) Hybridization of powdery mildew strains gives rise to pathogens on novel agricultural crop species. *Nature Genetics*, **48**, 202–205.
- Merritt, D.J. & Dixon, K.W. (2011) Restoration seed banks—A matter of scale. *Science*, **332**, 424–425.
- Millennium Ecosystem Assessment (2005) *Ecosystems and Human Well-Being: Desertification Synthesis*. World Resources Institute, Washington, DC, USA.
- Moir, W.H. & Block, W.M. (2001) Adaptive management on public lands in the United States: commitment or rhetoric? *Environmental Management*, **28**, 141–148.
- Moore, A.L. & McCarthy, M.A. (2010) On valuing information in adaptive-management models. *Conservation Biology*, **24**, 984–993.
- Munson, S.M. & Lauenroth, W.K. (2012) Plant community recovery following restoration in semiarid grasslands. *Restoration Ecology*, **20**, 656–663.
- Munson, S.M. & Lauenroth, W.K. (2014) Controls of vegetation structure and net primary production in restored grasslands. *Journal of Applied Ecology*, **51**, 988–996.
- Porensky, L.M., Leger, E.A., Davison, J., Miller, W.W., Goergen, E.M., Espeland, E.K. & Carroll-Moore, E.M. (2014) Arid old-field restoration: native perennial grasses suppress weeds and erosion, but also suppress native shrubs. *Agriculture, Ecosystems and Environment*, **184**, 135–144.
- Prach, K., Jongepierova, I., Rehoukova, K. & Fajmon, K. (2014) Restoration of grasslands on ex-arable land using regional and commercial seed mixtures and spontaneous succession: successional trajectories and changes in species richness. *Agriculture Ecosystems & Environment*, **182**, 131–136.
- Prach, K., Fajmon, K., Jongepierova, I. & Rehoukova, K. (2015) Landscape context in colonization of restored dry grasslands by target species. *Applied Vegetation Science*, **18**, 181–189.
- Prodders, R.A. (2013) Case study: fitness more than diversity guides vegetational recovery. *Journal of the American Society of Mining and Reclamation*, **2**, 113–141.
- Pyke, D.A., Wirth, T.A. & Beyers, J.L. (2013) Does seeding after wildfires in rangelands reduce erosion or invasive species? *Restoration Ecology*, **21**, 415–421.
- Rinella, M.J., Espeland, E.K. & Moffatt, B.J. (2016) Data from: studying long-term, large-scale grassland restoration outcomes to improve

- seeding methods and reveal knowledge gaps. *Dryad Digital Repository*, <http://dx.doi.org/10.5061/dryad.k5st3>
- Rinella, M.J., Mangold, J.M., Espeland, E.K., Sheley, R.L. & Jacobs, J.S. (2012) Long-term population dynamics of seeded plants in invaded grasslands. *Ecological Applications*, **22**, 1320–1329.
- Rinella, M.J., Hammond, D.H., Bryant, A.M. & Kozar, B.J. (2015) High precipitation and seeded species competition reduce seeded shrub establishment during dryland restoration. *Ecological Applications*, **25**, 1044–1053.
- Rumpff, L., Duncan, D.H., Vesk, P.A., Keith, D.A. & Wintle, B.A. (2011) State-and-transition modelling for adaptive management of native woodlands. *Biological Conservation*, **144**, 1224–1236.
- Runge, M.C. (2011) An introduction to adaptive management for threatened and endangered species. *Journal of Fish and Wildlife Management*, **2**, 220–233.
- Samuel, M.J. & Hart, R.H. (1998) Nitrogen fertilization, botanical composition and biomass production on mixed-grass rangeland. *Journal of Range Management*, **51**, 408–416.
- Schantz, M.C., Sheley, R.L. & James, J.J. (2015) Role of propagule pressure and priority effects on seedlings during invasion and restoration of shrub-steppe. *Biological Invasions*, **17**, 73–85.
- Sedinger, J.S. & Herzog, M.P. (2012) Harvest and dynamics of duck populations. *Journal of Wildlife Management*, **76**, 1108–1116.
- Soliveres, S., Moneris, J. & Cortina, J. (2012) Irrigation, organic fertilization and species successional stage modulate the response of woody seedlings to herbaceous competition in a semi-arid quarry restoration. *Applied Vegetation Science*, **15**, 175–186.
- Tischew, S., Baasch, A., Grunert, H. & Kirmer, A. (2014) How to develop native plant communities in heavily altered ecosystems: examples from large-scale surface mining in Germany. *Applied Vegetation Science*, **17**, 288–301.
- Torok, P., Deak, B., Vida, E., Valko, O., Lengyel, S. & Tothmeresz, B. (2010) Restoring grassland biodiversity: sowing low-diversity seed mixtures can lead to rapid favourable changes. *Biological Conservation*, **143**, 806–812.
- Vermeire, L.T., Heitschmidt, R.K. & Rinella, M.J. (2009) Primary productivity and precipitation use efficiency in mixed-grass prairie: a comparison of northern and southern U.S. sites. *Rangeland Ecology and Management*, **62**, 230–239.
- Walters, C.J. (1986) *Adaptive Management of Renewable Resources*. McGraw-Hill, New York, New York, USA.
- Walters, C.J. & Hilborn, R. (1978) Ecological optimization and adaptive management. *Annual Review of Ecology and Systematics*, **9**, 157–188.
- Walters, C.J. & Holling, C.S. (1990) Large-scale management experiments and learning by doing. *Ecology*, **7**, 2060–2068.
- Ward, D., Wiegand, K. & Getzin, S. (2013) Walter's two-layer hypothesis revisited: back to the roots!. *Oecologia*, **172**, 617–630.
- Weiner, J. & Freckleton, R.P. (2010) Constant final yield. *Annual Review of Ecology and Systematics*, **41**, 173–192.
- Williams, M.I., Schuman, G.E., Hild, A.L. & Vicklund, L.E. (2002) Wyoming big sagebrush density: effects of seeding rates and grass competition. *Restoration Ecology*, **10**, 385–391.
- Wilson, M.V., Ingersoll, C.A., Wilson, M.G. & Clark, D.L. (2004) Why pest plant control and native plant establishment failed: a restoration autopsy. *Natural Areas Journal*, **24**, 23–31.

Received 10 February 2016; accepted 16 June 2016

Handling Editor: Jeremy James

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Exotic perennial grass time trends.

Appendix S1. Analytical details.