

High precipitation and seeded species competition reduce seeded shrub establishment during dryland restoration

MATTHEW J. RINELLA,^{1,5} DARCY H. HAMMOND,² ANA-ELISA M. BRYANT,³ AND BRIAN J. KOZAR⁴

¹Fort Keogh Livestock and Range Research Laboratory, United States Department of Agriculture, Agricultural Research Service, 243 Fort Keogh Road, Miles City, Montana 59301 USA

²Department of Forestry, College of Forest Resources, Mississippi State University, Mississippi State, Mississippi 39759 USA

³Center for Leadership in Global Sustainability, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061 USA

⁴Terra Soil and Environmental Solutions, Bozeman, Montana 59714 USA

Abstract. Drylands comprise 40% of Earth's land mass and are critical to food security, carbon sequestration, and threatened and endangered wildlife. Exotic weed invasions, overgrazing, energy extraction, and other factors have degraded many drylands, and this has placed an increased emphasis on dryland restoration. The increased restoration focus has generated a wealth of experience, innovations and empirical data, yet the goal of restoring diverse, native, dryland plant assemblages composed of grasses, forbs, and shrubs has generally proven beyond reach. Of particular concern are shrubs, which often fail to establish or establish at trivially low densities. We used data from two Great Plains, USA coal mines to explore factors regulating shrub establishment. Our predictor data related to weather and restoration (e.g., seed rates, rock cover) variables, and our response data described shrub abundances on fields of the mines. We found that seeded non-shrubs, especially grasses, formed an important competitive barrier to shrub establishment: With every one standard deviation increase in non-shrub seed rate, the probability shrubs were present decreased ~ 0.1 and shrub cover decreased $\sim 35\%$. Since new fields were seeded almost every year for >20 years, the data also provided a unique opportunity to explore effects of stochastic drivers (i.e., precipitation, year effects). With every one standard deviation *increase* in precipitation the first growing season following seeding, the probability shrubs were present *decreased* ~ 0.07 and shrub cover *decreased* $\sim 47\%$. High precipitation appeared to harm shrubs by increasing grass growth/competition. Also, weak evidence suggested shrub establishment was better in rockier fields where grass abundance/competition was lower. Multiple lines of evidence suggest reducing grass seed rates below levels typically used in Great Plains restoration would benefit shrubs without substantially impacting grass stand development over the long term. We used Bayesian statistics to estimate effects of seed rates and other restoration predictors probabilistically to allow knowledge of the predictors' effects to be refined through time in an adaptive management framework. We believe this framework could improve restoration planning in a variety of systems where restoration outcomes remain highly uncertain and ongoing restoration efforts are continually providing new data of value for reducing the uncertainty.

Key words: Bayesian adaptive management; competition; dryland; grassland; restoration; seeding; shrub.

INTRODUCTION

Dryland ecosystems comprise $\sim 40\%$ of Earth's land area (O'Mara 2012) and are critical for food security, carbon sequestration, and other values (Millennium Ecosystem Assessment 2005). Exotic species invasions, overgrazing, mining, agriculture, and other factors have extensively degraded dryland ecosystems throughout the world (e.g., Knapp 1996, Jones and Schmitz 2009, Merritt and Dixon 2011, James et al. 2013). Recent decades have ushered in major efforts to reverse this

degradation, but these efforts have proven highly prone to failure (Wilson et al. 2004, MacDougall et al. 2008, Rinella et al. 2012, James et al. 2013, Fehmi et al. 2014). Of the three major plant groups comprising dryland plant communities (grasses, forbs, shrubs), restoration of shrubs has proven most failure prone. When sown with grasses, shrubs often nearly or completely fail to establish (e.g., Bailey et al. 2010, Fansler and Mangold 2011, Kulpa et al. 2012, Schellenberg et al. 2012). Consequently, "restored" drylands often have adequate grass stands but no shrubs or far fewer shrubs than nearby reference sites (Booth et al. 1999, Simmers and Galatowitsch 2010, Frouz et al. 2013). A need to restore shrubs is being increasingly recognized in many parts of the world, including Africa (Linstadter and Baumann

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⁵ E-mail: Matt.rinella@ars.usda.gov

2013), Australia (Wong et al. 2007), China (Li et al. 2013a), Europe (Medina-Roldán et al. 2012), and the United States (Davies et al. 2011). Attention is focusing on shrub species that provide forage for livestock (Fang et al. 2006) and wildlife (Ngugi et al. 1992), habitat for threatened and endangered shrub-obligate fauna (Rowland et al. 2006, Hanser and Knick 2011), and soil stabilization to address desertification issues (Li et al. 2013b, Linstadter and Baumann 2013).

Until shrubs and other seeded dryland plants approach mature sizes, their fates are closely regulated by water availability (Bakker et al. 2003, Wilson et al. 2004), weed competition (Masters and Nissen 1998, Bakker and Wilson 2001) and other widely varying stochastic drivers that cannot generally be predicted or cost-effectively controlled. These stochastic drivers can cause restoration plans (i.e., combination of seed rates, herbicides, tillage, etc.) to give quite different outcomes each time they are applied (Bakker et al. 2003, Wilson et al. 2004, Vaughn and Young 2010, Boyd and James 2013). This wide variability of results has made it conceptually appealing to describe dryland restoration outcomes probabilistically (James et al. 2013). In practice, however, the probability any given restoration outcome (e.g., shrub cover, shrub density) will be realized is highly uncertain, and there have been no statistical attempts to estimate these probabilities for drylands.

If developed, probabilistic estimates of restoration outcomes could prove invaluable in restoration planning. Probabilistic estimates are required for economically rational decision-making, because the amounts that can be rationally invested in restoration depend on the probability desired restoration outcomes will be achieved (James et al. 2013). Also, probabilistic estimates play a central role in adaptive management, an approach to natural resource decision-making under uncertainty (Holling 1978, Walters and Hilborn 1978). In Bayesian adaptive management, data describing past management actions and outcomes are used to develop models that probabilistically predict future management outcomes (e.g., Prato 2005, Rout et al. 2009). These predictions represent hypotheses based on current understanding of the system. When new data become available, the models (i.e., hypotheses) are updated via Bayes formula, and in this way uncertainty about responses to various management alternatives declines as sample sizes increase through time. In drylands, prediction uncertainty regarding plant abundances (e.g., shrub cover) could be described using Bayesian confidence intervals, and reductions in uncertainty would manifest as a narrowing of these intervals in response to new data. This is an attractive scheme for improving predictive capabilities in systems such as Great Basin, USA, rangelands (Davies et al. 2011) and surface coal mines (Booth et al. 1999) where ongoing restoration efforts regularly provide opportunities to gather new

data useful for refining predictions of restoration outcomes.

Without the extensive data that ongoing, large-scale, restoration efforts are capable of providing, it is unclear how probabilistic estimates of restoration outcomes could ever be developed, because typical restoration experiments comprised of small numbers of treatments applied to small plots at one or two sites with no temporal replication do not provide sufficiently rich data (Vaughn and Young 2010). In this study, we worked with data from two Montana, USA coal mines to develop probabilistic estimates of shrub restoration outcomes. Multiple fields of the mines were subjected to restoration attempts almost every year for over 20 years, so the data include considerable temporal and spatial replication. Moreover, Montana law requires coal mines to keep records on seed rates, soil depths, tillage practices, and other reclamation inputs (Montana Department of Environmental Quality, Administrative Rules [Title 17]). These records, along with weather observations, constituted our predictor data, and we generated our response data by sampling the fields' shrub abundances. Our first objective was to identify important managerial and stochastic predictors regulating dynamics of seeded shrubs, the most difficult plant group to restore in the Great Plains and many other dryland ecosystems. Our second objective was to estimate effects of these predictors probabilistically. We discuss how probabilistic estimates could be used in an adaptive management framework to refine restoration strategies through time.

MATERIALS AND METHODS

Restoration procedures

The two northern Great Plains surface coal mines we studied were Decker and Spring Creek, which are located 35 and 56 km north of Sheridan, Wyoming, respectively. We included in our study 134 Decker fields and 35 Spring Creek fields, with a field being a contiguous area uniformly treated with the same restoration inputs (e.g., seed rates, tillage practices) across its entire expanse over a short period of time, typically days. As we will explain in detail, some fields with poor vegetation development received follow-up restoration activities (e.g., reseeding) after initial seeding. Data from these fields proved useful in an auxiliary analysis, but they were excluded from our analysis of shrub abundance data. Therefore, the fields used in our shrub analysis received no additional inputs after receiving a preplanned set of restoration treatments at a single point in time. Fields ranged in size from 0.2 to 19.9 ha and were seeded between 1992 and 2009.

The restoration process began with the spreading of crushed material derived from rock layers that formerly overlaid the coal seams. This material was deposited so as to reconstruct pre-mining topography. Then, topsoil removed during mining of other area(s) was spread over the crushed rock. After topsoil spreading, fields often

TABLE 1. Combinations of shrub species seeded to fields during restoration of coal mining lands.

| No. fields | Big sage | Fringed sage | Four-wing saltbush | Winterfat |
|------------|----------|--------------|--------------------|-----------|
| 1 | | x | | |
| 1 | | | x | |
| 2 | | x | x | |
| 2 | | x | x | x |
| 4 | x | x | x | |
| 10 | x | | x | |
| 12 | x | x | | |
| 14 | x | x | x | x |
| 46 | x | | x | x |

remained fallow for weeks or months. Then, just prior to seeding, fields were often tilled. With the exception of winter wheat (*Triticum aestivum* L.) and spring barley (*Hordeum vulgare* L.), which were used as cover crops in some fields, and sheep fescue (*Festuca ovina* L.), which was sown in some Spring Creek fields, seed mixes were composed entirely of native grasses, forbs, and shrubs. After seeding, monitoring took place for several years to determine if vegetation goals were being met or if follow up measures were required to increase seeded species abundances and control weedy species such as Kochia (*Kochia scoparia* L.) and cheatgrass (*Bromus tectorum* L.).

Restoration history data

Restoration records provided by the mines recorded topsoil depth, tillage methods (disking, ripping, cultipacking, harrowing, or combination of these), seeding year and season (fall, spring), seeding method (drilled, broadcast, or combination of these), pure live seed (pls) rates (kg pls/ha) of restoration forbs, grasses, and shrubs, as well as any cover crops (spring barley, winter wheat) seeded around the time restoration species were seeded. Records also indicated if topsoils were stored in piles for extended periods prior to spreading or came directly from newly mined areas. Finally, mine records provided details on any follow up measures employed after the initial seeding. Precipitation data came from the nearest National Oceanic and Atmospheric Administration weather station in Decker, Montana.

Sampling methods

Sampling plots measuring 4.6 × 45.7 m were equally spaced along the longest possible transect in each field. The number of plots per field depended on how many would fit along the transect, with one, two, and three plots occurring in 9%, 20%, and 71% of Decker fields and 4%, 96%, and 0% of Spring Creek fields, respectively. In summer 2012, we estimated cover of the shrubs big sage (*Artemisia tridentata* Nutt.), fringed sage (*Artemisia frigida* Willd.), winterfat (*Krascheninnikovia lanata* (Pursh) A. Meeuse and Smit), and four-wing saltbush (*Atriplex canescens* (Pursh) Nutt.) by counting numbers of shrubs per plot and measuring widths of

individual shrubs. Widths were measured in two random perpendicular directions on the first five individuals encountered per species, if five individuals occurred in the plot. Average area per individual was estimated by interpreting average widths as diameters and applying the circle area formula. Cover of each shrub species in each plot was estimated by multiplying individuals per plot by average area per individual and dividing by plot area. We visually estimated cover of rock, seeded forbs and seeded grasses in three 20 × 50 cm frames evenly spaced across each plot.

Statistical modeling

In estimating effects of restoration variables on shrub abundances, we excluded 65 Decker and 12 Spring Creek fields that received follow up measures (i.e., prescribed fire, herbicide, mowing, tillage, reseeding) after initial seeding. These fields were excluded because follow-up measures were nonrandomly assigned only to fields exhibiting poor seeded grass establishment. Therefore, the decision to apply follow up measures represents a “post-treatment” variable, and both conditioning on and ignoring post-treatment variables can invalidate causal inferences (Gelman and Hill 2007: chapter 9). Because fields subjected to follow up restoration activities were excluded, our inferences are restricted to fields not receiving these activities.

After removing fields that received follow up restoration activities, 92 fields seeded with various mixtures of shrubs remained in the dataset (Table 1). The dataset contained many zeros, because no shrubs occurred in sample plots of 22 of 92 fields. To model this mixture of zeros and continuous shrub cover data we employed a commonly used two-stage approach (Gelman and Hill 2007). The first stage model estimated the probability a shrub species seeded in a field was observed in plots of that field, and the second stage modeled shrub cover conditional on the species being observed. The first stage model was the probit model

$$\begin{aligned}
 &Pr(y_i = 1) \\
 &= \Phi \left(\alpha_{1,j(i)} + \alpha_{2,k(i)} + \alpha_{3,l(i)} + \alpha_{4,m(i)} + \sum_{n=5}^{10} \alpha_n x_{n-4,i} \right)
 \end{aligned}
 \tag{1}$$

where $\Phi()$ denotes the normal distribution function with its argument being the mean and the standard deviation being 1.0 (Albert and Chib 1993, Greenberg 2008). The response, y_i , equaled 1 if the shrub species given by indicator function $k(i)$ occurred in one or more sample plots of the field given by indicator function $m(i)$ and otherwise equaled 0. Parameters are effects of mines ($\alpha_{1,j}$), shrub species ($\alpha_{2,k}$), interactions between shrub species and the year of the first growing season following seeding ($\alpha_{3,l}$), and field ($\alpha_{4,m}$). Other parameters (i.e., α_5 through α_{10}) multiply continuous predictors (x). These

predictors, which were standardized to mean 0 standard deviation 1, are elapsed years between seeding and 2012 for four-wing saltbush and big sage (x_1), this same elapsed time variable for fringed sage (x_2), precipitation in the first 1 April–31 July period to occur following seeding (x_3), total seed rate of cover crops plus other grasses and forbs (x_4), rock cover (x_5), and shrub seed rate of species $k(i)$ (x_6). The combined four-wing saltbush, big sage time trend (x_1) was included because, with this time trend omitted from the model, scatter plots showed these species exhibited similar positive relationships between time since seeding and $\hat{\alpha}_{3,i}$'s. The fringed sage time trend (x_2) was included because, with this time trend omitted, scatter plots suggested an inverse relationship between time since seeding and $\hat{\alpha}_{3,i}$'s for this species. A winterfat time trend was not necessary to capture patterns in the data, likely because the bulk of seeding occurred in a narrower range of years for winterfat than the other shrubs. The 1 April–31 July precipitation period was used because this is when >90% of dryland plant growth occurs in the northern Great Plains (Vermeire et al. 2009), and precipitation during this period has been shown to regulate germination and survival of seeded dryland plants in the region (Bakker et al. 2003). Expanding the precipitation period several months provided very similar inferences. The second stage model for the 70 fields in which shrubs were observed in sample plots was

$$\ln(z_i) = N \left(\beta_{1,j(i)} + \beta_{2,k(i)} + \beta_{3,l(i)} + \beta_{4,m(i)} + \sum_{n=5}^{10} \beta_n x_{n-4,i}, \sigma \right) \quad (2)$$

where z_i is shrub cover of species $k(i)$ in field $m(i)$, and $N(\cdot)$ is the normal density function with the arguments before and after the comma being the mean and standard deviation, respectively. The parameters β_1 through β_{10} model the same effects as the parameters α_1 through α_{10} , respectively.

Other variables, besides those of Eqs. 1 and 2, were evaluated in preliminary versions of the models. These variables related to tillage and seeding methods, topsoil depth and source (stored vs. directly relocated topsoil), seeding season (fall, spring), additional time trends, shrub species \times seed rate interactions, and, in the case of Eq. 1, the number of sample plots per field. These variables were ultimately excluded from the models because confidence intervals on their effects were centered near zero. Moreover, point estimates of Eqs. 1 and 2 parameters were not highly sensitive to the inclusion/exclusion of these variables. A number of posterior predictive checks were used to assess model fit and the ability of the models to capture important features of the data (Gelman et al. 2004). This involved comparing features of the observed data to synthetic

data generated from the fitted model and elaborating the model where necessary to alleviate discrepancies between the two data sources.

Our Bayesian approach to probabilistically estimating parameters of Eqs. 1 and 2 required assigning prior probability distributions to the parameters. Priors on shrub seed rate parameters, α_9 and β_9 , were uniform on $(0, \infty)$, owing to the implausibility of inverse relationships between shrub seed rates and shrub cover in this study system. Standard non-informative priors were assigned to all other parameters (Gelman et al. 2004). Specifically, priors on α_1 , α_5 , α_6 , α_7 , and α_8 and β_1 , β_5 , β_6 , β_7 , and β_8 were uniform with support on the whole real line. Priors on α_2 , α_3 , and α_4 were normal with mean 0, standard deviation τ_1 and τ_2 , respectively. Priors on β_2 , β_3 , and β_4 were normal with mean 0, standard deviation τ_3 and τ_4 , respectively. Priors on each τ were uniform on the whole real line and on the random error variance was $p(\sigma^2) \propto 1/\sigma^2$. We constructed Markov chain Monte Carlo (MCMC) algorithms (i.e., Gibbs samplers) in FORTRAN to simulate the posterior distributions (Gelman et al. 2004).

To better understand estimates from Eqs. 1 and 2, we fit two additional models. One model was a linear regression with the natural log of seeded grass cover as the response, and the other was a probit model that estimated the probability fields had to be reseeded due to low grass establishment. Both models had year of the first growing season following seeding as a random effect and precipitation in that same growing season, rock cover, grass seed rate, and mine as fixed effects. The precipitation, rock, and grass seed rate variables were standardized to mean 0, standard deviation 1.

We based inferences on features of the posterior probability distributions. Specifically, inferences were based on 95% Bayesian confidence intervals (CI) and probabilities effects were positive or negative (Pr).

RESULTS

Shrub cover varied widely but in most fields was low (Fig. 1A–D). Averaged across shrub species, the probability of shrub presence was 0.33 [0.15–0.51] (point estimate followed by 95% confidence interval) in Decker fields and 0.7 [0.46–0.88] in Spring Creek fields. Within fields where shrubs were present, mean cover per shrub species was 0.6% [0.2–2.2%] and 5.5% [1.2–21.9%] for Decker and Spring Creek, respectively. After controlling for model variables, there was little evidence that shrub presence/absence differed greatly by species (Fig. 2). There was weak evidence that fringed sage had the least cover, which is logical given this species' comparatively small stature (Fig. 2).

Shrub seed rates varied widely among fields (Fig. 1E–H), but effects of shrub seed rates on shrub presence were relatively small (Fig. 2). More than doubling the shrub seed rate from 1.0 to 2.3 kg pls/ha increased the probability of shrub presence no more than 0.1 (Fig. 3). This same increase in shrub seed rate increased shrub

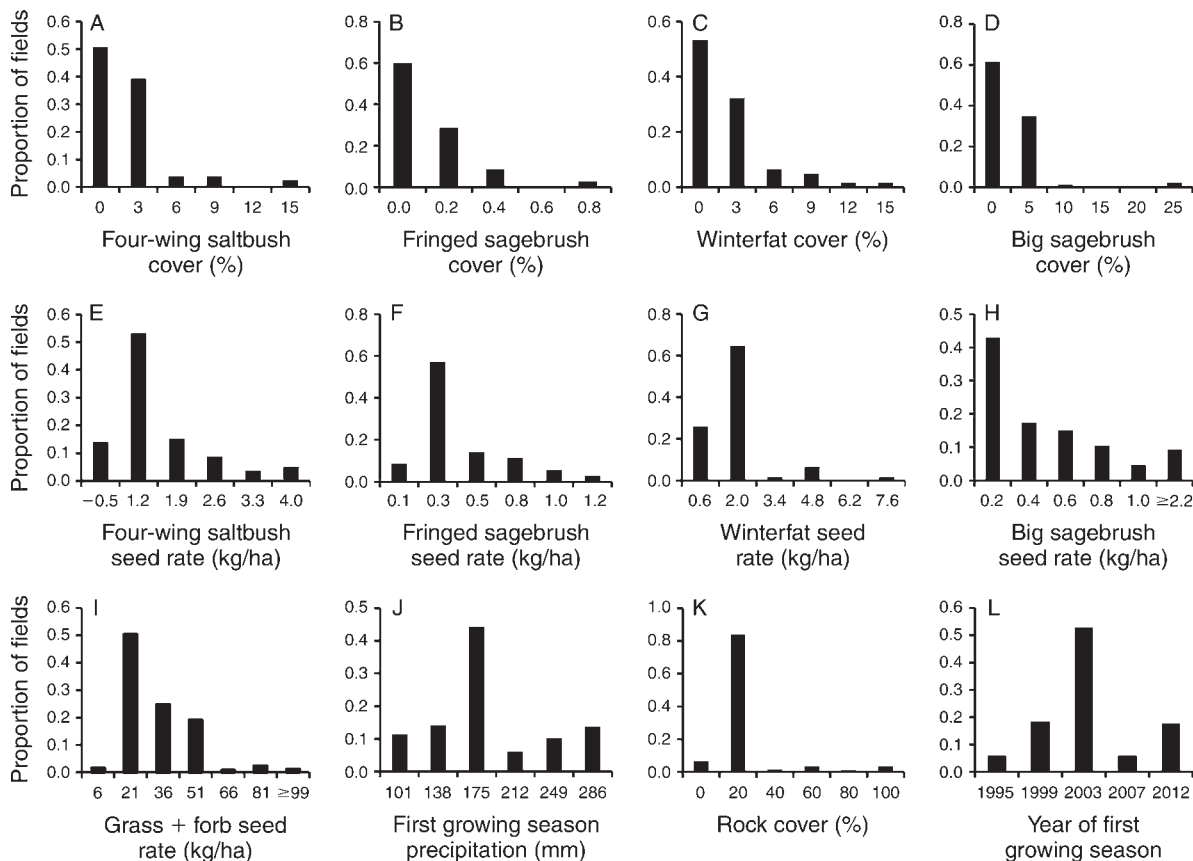


FIG. 1. Histograms showing proportions of fields of former coal mining lands having particular values for shrub cover, shrub pure live seed rates, combined grass and forb pure live seed rates, precipitation during the first growing season (1 April–31 July) after seeding, rock cover, and year of the first growing season after seeding.

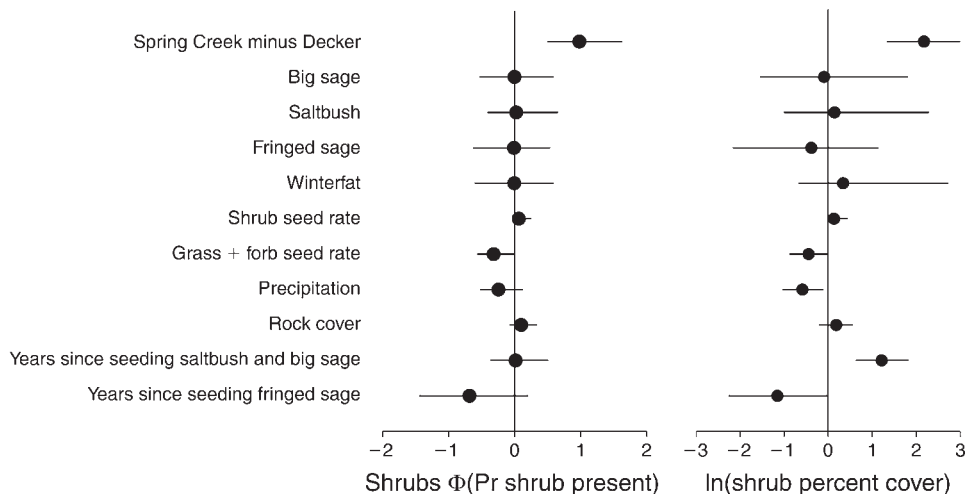


FIG. 2. Point estimates (dots) and 95% confidence intervals (lines) on parameters of models used to estimate the probability that shrubs were present and shrub cover on fields of former coal mining lands, where $\Phi()$ denotes the normal distribution function with its argument being the mean and the standard deviation being 1.0. Parameters describe differences in mean shrub cover between Spring Creek and Decker mines and effects of shrub species, shrub pure live seed (pls) rate (kg pls/ha), combined pls rate of forbs and grasses (kg pls/ha), precipitation during the first growing season (1 April–31 July) after seeding (mm), rock cover (%), years since saltbush and big sage seeding, and years since fringed sage seeding. Except for categorical variables (i.e., mine, shrub species), variables were standardized to mean 0, standard deviation 1.0 to make them directly comparable.

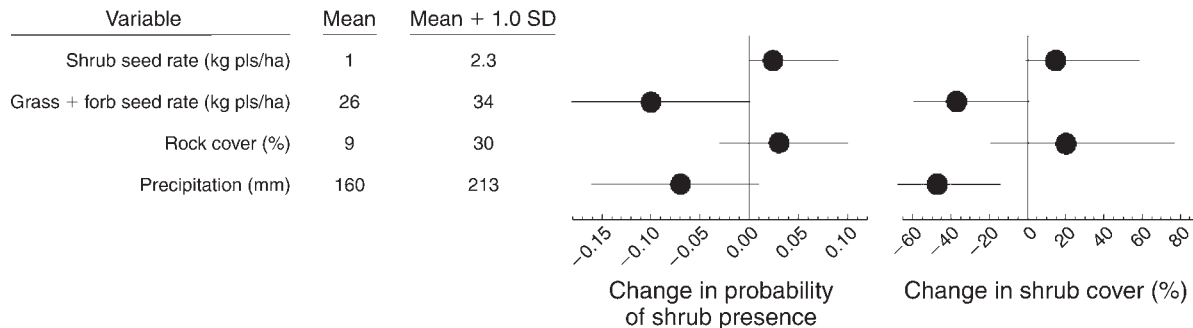


FIG. 3. Point estimates (dots) and 95% confidence intervals (lines) estimating effects of increasing variables one standard deviation above their mean on (1) the probability that shrubs were present and (2) shrub cover. Variables are shrub pure live seed (pls) rate (kg pls/ha), combined grass and forb pls rate (kg pls/ha), rock cover (%), and precipitation during the first growing season (1 April–31 July) after seeding (mm).

cover no more than 77%, and the most likely increase was 16%.

As with shrub seed rates, non-shrub seed rates also varied appreciably among fields (Fig. 1I), and shrub presence ($Pr > 0.99$) and cover ($Pr = 0.97$) decreased with increasing non-shrub seed rate (Fig. 3). Shrub presence ($Pr = 0.96$) and cover ($Pr > 0.99$) increased with decreasing precipitation the first growing season following seeding (Figs. 1J, 2). There is weak evidence that both shrub presence ($Pr = 0.85$) and cover ($Pr = 0.84$) increased with increasing rock cover (Figs. 1K, 3), while seeded grass cover decreased with increasing rock cover ($Pr > 0.99$). In particular, fields with 1 standard deviation above mean rock cover had 25% [40–10%] lower grass cover.

The big sage/saltbush time trend estimate suggests these species' cover increased through time. Every one year increment in time since seeding was associated with a 29% [13–47%] increase in big sage/saltbush cover (Figs. 1L, 2). This suggests any big sage/saltbush mortality that occurred was more than offset by increases in plant size and perhaps recruitment. Conversely, the model indicated less fringed sage in older fields (Fig. 2), suggesting either fringed sage populations decreased through time or fringed sage restoration methods improved over time for reasons not captured by the model.

Shrub abundances were greatly influenced by factors not included in the models. The error rate for the shrub presence/absence model was 26%, implying Eq. 1 correctly predicted shrub presence/absence in just 74% of cases. This high error rate demonstrates that un-modeled factors played important roles in regulating shrub presence/absence. The shrub cover model likewise highlights the importance of un-modeled factors. To see this, we worked with the point estimate of the residual error standard deviation (1.8) and the mean Spring Creek predictor variable values. Accordingly, mean shrub cover minus and plus 1 standard deviation was 0.8% and 31%, respectively. Thus, shrub cover had the potential to vary dramatically, even among fields

exposed to the same environmental conditions and recorded restoration procedures.

DISCUSSION

Our study provides strong evidence that seeded non-shrubs formed a competitive barrier to shrub establishment (Fig. 3). Most competition likely came from seeded grasses, which made up 86% [85–87%] of combined seeded forb and grass cover. The shrub and grass species of our study tend to germinate rapidly when exposed to favorable environmental conditions (e.g., Bai and Romo 1994, Schuman et al. 1998, Qiu et al. 2008). Thus, sown grass and shrub seeds likely tended to germinate around the same time, and it appears many of the shrub seedlings were often outcompeted by the developing grasses.

Two studies support our findings by reporting much greater dryland shrub densities and biomass where perennial grasses were not seeded compared to where they were seeded (Blaisdell 1949, Hubbard 1957). A third study further supports our findings by reporting greater transplanted shrub cover in plots where a perennial grass species failed to establish compared to plots where other perennial grass species successfully established (Porensky et al. 2014). In all three of these studies, weedy annual species were present at the study sites, and this suggests that, compared to weedy annuals, perennial grasses may form a stronger competitive barrier to shrub establishment (Wilson et al. 2004). All three of these studies were conducted in the Great Basin, a different dryland system than the one we studied, and this suggests perennial grass competition may be a general factor constraining dryland shrub establishment. However, the intensity of grass competition with shrubs could vary appreciably across dryland systems, as could other relationships we observed in our study.

Our results suggest lowering grass seed rates might be the simplest way to increase shrub establishment, though it seems weed invasions could result if seeded grasses were slow to colonize large gaps resulting from lower grass seed rates. Moreover, grass seedling emergence

and survival vary with weather conditions (e.g., Bakker et al. 2003, Boyd and James 2013), so one might infer that high grass seed rates are needed to guard against possibly poor conditions. However, our data embody the wide-ranging weather conditions of a 17-year period (Fig. 1J), and a wide range of perennial grass seed rates (3–40 kg pls/ha), and we observed no evidence that grass cover increased with increasing grass seed rate ≥ 3 years after seeding ($Pr = 0.31$). Additionally, we observed no evidence that increasing grass seed rates reduced the probability fields would require reseeding due to poor grass establishment ($Pr = 0.30$). Thus it appears fields receiving widely differing grass seed rates eventually converged at similar grass abundances. Prior to this convergence, fields sown at lower grass rates have less grass, and this seems to encourage shrub establishment. A small Great Plains coal mine restoration study supports this view. Williams et al. (2002) studied grass seed rates of 2, 4, 6, 8, 10, and 14 kg pls/ha. Grass biomass started out lower for the lower seeding rates but eventually became statistically equivalent for all grass seed rates. The 14 kg pls/ha rate sharply reduced big sage densities and there was an inverse relationship between grass seed rate and big sage plant size (Williams et al. 2002, Hild et al. 2006). It appears grass seed rates at or below the low end of the 3–40 kg pls/ha range we studied may be sufficient for Great Plains restoration. Booth et al. (1999) reported perennial grass seed rates of 15–30 kg pls/ha were used at eight Great Plains coal mines, indicating grass rates uncondusive to shrub establishment are commonly used in our study system.

In addition to lowering grass seed rates, our study highlighted other potential avenues for reducing competitive effects of grasses on shrubs. One approach might involve seeding shrubs before grasses. Blaisdell (1949) compared shrubs sown two years before grasses to shrubs sown with grasses and found shrubs seeded before grasses produced roughly twice the biomass. The risk in this approach is that weedy annual species would likely flourish in the interval between shrub and grass seeding, and these weeds could prevent grass establishment. The extent of this risk is unclear, however. Besides Blaisdell (1949), at least one other study successfully established grasses in existing shrub stands (Huber-Sannwald and Pyke 2005). Another way to reduce grass competition during shrub establishment would be to introduce cattle or other grazers that prefer grasses to shrubs. Grass herbivory has been shown to increase shrub establishment in some systems (e.g., Van Auken 2000, Whitford et al. 2001).

Dry conditions favored shrubs in our study (Fig. 3), and an auxiliary analysis of reseeded fields excluded from our main analysis supports our hypothesis that this occurred because dry conditions reduced grass competition. Reseeding was restricted to fields where grasses failed to establish, and the auxiliary analysis suggested the probability fields were reseeded increased with decreasing establishment precipitation ($Pr = 0.92$). If

dry conditions could sometimes outright prevent grass establishment, it seems dry conditions could sometimes also slow grass establishment and thereby favor shrubs. Similar to our study, two other studies have reported greater shrub establishment in un-irrigated than irrigated plots owing to lower grass competition in the un-irrigated plots (Doerr et al. 1983, Soliveres et al. 2012). However, another study found no significant differences in transplanted shrub abundances between irrigated and unirrigated plots (Porensky et al. 2014). Shrub species can establish in atypically dry periods (Brown and Archer 1989, Brown and Archer 1999, Matias et al. 2012, del Cacho et al. 2013), whereas grass seedling mortality can be 100% in dry years (Lauenroth et al. 1994, Bakker et al. 2003). This may be because shrub roots quickly penetrate soils to extract water below grass rooting zones (Brown and Archer 1990, Kambatuku et al. 2013).

Our rock cover data further suggest seeded grasses negatively impacted shrubs. As rock cover increased, seeded grass cover decreased ($Pr > 0.99$), and shrub presence ($Pr = 0.85$) and cover ($Pr = 0.84$) may have increased. Other studies have reported that rocky soils have greater shrub abundances (Hodge and Harper 1996, Maestre et al. 2003, Britz and Ward 2007, Svoray et al. 2007, Ward and Esler 2011) and lower grass abundances (Mbatha and Ward 2010, Ward and Esler 2011, Ward and Mervosh 2012) than fine soils. Kambatuku et al. (2013) found rocky soils helped seedlings of a woody species acquire water and nutrients from deeper in soils than grasses. In systems where physical soil properties can be manipulated, adding rocky overburden material to topsoil may reduce grass production and thereby enhance shrub restoration efforts.

Bayesian adaptive restoration management

Bayesian adaptive management has been applied in endangered species protection (e.g., Rout et al. 2009, McDonald-Madden et al. 2010) and a variety of other natural resource areas (Moore and McCarthy 2010, Rumpff et al. 2011, Fukasawa et al. 2013). However, despite showing promise in these areas, many resource managers remain unenthusiastic about model-based adaptive management (Allan and Curtis 2005, Gregory et al. 2006, Addison et al. 2013). One reason for this is that data and knowledge accumulate slowly in typical adaptive management programs because the programs usually involve only one or few management units (e.g., populations, sites, watersheds) subject to only one or few independently assessable management plans at a time (Gregory and Failing 2002, Gregory et al. 2006). Learning could occur more rapidly in ours and other dryland systems owing to greater data availability. For example, we recently compiled restoration history data from nine Great Plains coal mines, which is but a fraction of the region's mines. These data indicate 22 seed mixes were applied in 1992 alone, and the data also

indicate variation in other restoration variables (e.g., seeding, tillage and mulching methods). All these mines remain in operation and attempt restoration of new fields most years. If vegetation variables were measured at these mines, large datasets for modeling a variety of restoration responses of interest (e.g., species richness, weed abundances) could be assembled rather quickly. Other dryland systems with data sufficient to support analyses similar to ours include degraded Great Basin, USA, rangelands (Eiswerth et al. 2009) and likely mined grasslands of Australia (Vickers et al. 2012) and Europe (Tischew et al. 2014).

To exhibit how adaptive management might proceed in our system, we note that predictions of future shrub abundances in yet-to-be-seeded fields can be generated by assigning values to predictors of Eqns. 1 and 2 and running our MCMC algorithms. Currently, uncertainty in these predictions is considerable owing in part to high parameter uncertainty (Figs. 2, 3). Gathering shrub abundance data from new fields of our study mines and/or fields of other regional mines would allow for periodic Bayesian updating of our model's parameters, which in practice would entail combining the new and existing datasets and refitting the model. Thus, as data accumulate, the model could be made to generate more precise predictions of shrub abundances resulting from candidate restoration plans. To the extent the predictions are used to refine management plans, our model could form the basis for a "passive" adaptive management program. In passive adaptive management, learning is a by-product of monitoring responses to common, slowly evolving management plans (Walters and Holling 1990). In our system, learning could comprise quantifying effects of shifts toward lower grass seed rates, for example.

Our system seems particularly amenable to "active," as well as passive, adaptive management (Walters and Holling 1990). In active adaptive management, decision-making reflects a balance between effective short-term management and experimental management strategies selected to improve knowledge of the system and thereby improve management over the long term. It is difficult to engage stakeholders in active adaptive management when experimental management strategies have grave potential consequences, such as in endangered species management (Gregory et al. 2006). In our system, the consequences of failed restoration are comparatively mild because each effort involves a fairly small (~1–20 ha) area that can be retreated if restoration fails. Thus there is relatively low risk in experimenting with unconventional shrub restoration strategies in our system. And unconventional strategies seem warranted, because shrubs often nearly or completely fail to establish with currently used strategies (e.g., Padgett et al. 2000, Fansler and Mangold 2011, Davies et al. 2013, Knutson et al. 2014). This is particularly concerning in the region we studied where shrubs are a major source of food and habitat for wild

ungulates (Wambolt 1996, Jacques et al. 2006) and the loss of big sage populations has contributed to Greater Sage-Grouse (*Centrocercus urophasianus*) becoming a candidate for listing under the endangered species act (U.S. Fish and Wildlife Service 2010, Taylor et al. 2013). In addition to Greater Sage-Grouse, sagebrush ecosystems have many other obligate species (Rowland et al. 2006). Given these considerations, and the high cost of shrub seeds (Schuman et al. 2005), the low success of shrub restoration efforts seems unsustainable, and broad changes to shrub restoration practices seem justified.

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SUPPLEMENTAL MATERIAL

Data Availability

Data associated with this paper have been deposited in Dryad: <http://dx.doi.org/10.5061/dryad.b91t7>