Rangeland Ecology & Management 70 (2017) 477–483

Contents lists available at ScienceDirect

Rangeland Ecology & Management

journal homepage: http://www.elsevier.com/locate/rama

Original Research

Seed Bank Depletion: The Key to Long-Term Downy Brome (*Bromus tectorum* L.) Management

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ARTICLE INFO

Article history:
Received 11 July 2016
Received in revised form 13 December 2016
Accepted 22 December 2016

Key Words:
cheatgrass
downy brome
imazapic
indaziflam
restoration
seed bank

ABSTRACT

Invasive winter annual grasses such as downy brome (*Bromus tectorum* L.) are a threat to native ecosystems throughout the United States. Downy brome is able to exploit moisture and nutrients throughout the fall and early spring before native plants break dormancy. This results in decreased native species abundance and development of monotypic downy brome stands. Short-term downy brome management has been shown to be effective; however, the soil seed reserve has often been overlooked, although it's the mechanism responsible for rapid reestablishment. This field study was conducted at two sites in Colorado to evaluate the longevity of the downy brome soil seed reserve and its implications on long-term downy brome control. Glyphosate plus adjuvant applications were made for 0, 1, 2, 3, 4, or 5 consecutive years. Downy brome and perennial grass biomass harvests were conducted yearly to determine changes in species composition. In addition, soil cores were collected to evaluate the yearly variation and depletion of the downy brome soil seed bank in response to consecutive glyphosate applications. We found that 1 − 3 yr of consecutive glyphosate treatments were insufficient to deplete the downy brome soil seed bank. Downy brome biomass and the soil seed bank recovered within 1 − 2 yr after glyphosate treatments were terminated; however, 4 and 5 consecutive yr of glyphosate applications were sufficient to control downy brome through depletion of the soil seed bank. Managing downy brome for 4 − 5 consecutive yr resulted in a 4- to 9-fold increase in perennial grass biomass. These data suggest that long-term management of downy brome is dependent on eliminating the soil seed bank using a multiyear approach.

Introduction

Downy brome (*Bromus tectorum* L.) is one of the most researched invasive weed species on rangeland. A Web of Science search identified 1 057 citations containing the words "downy brome" or "*Bromus tectorum*" since 1990, with 79% of the citations occurring between 2000 and 2016. This suggests that concerns about downy brome's many ecological and economic impacts are increasing (Ogle et al., 2003; Crawford et al., 2004; Duncan et al., 2004). There is evidence that some of these impacts could be approaching the point where they are no longer reversible (D'Antonio and Vitousek, 1992; DiTomaso, 2000; Rimer and Evans, 2006; Balch et al., 2013; Chambers et al., 2014).

There is limited research on the implications of managing the downy brome soil seed bank on long-term control. This is a crucial aspect for managing invasive species that reproduce only by seed, such as downy brome; however, reestablishment via the soil seed bank is often overlooked or not well understood. Downy brome is a winter annual grass species that commonly germinates in the fall; however, downy brome can behave more like a spring annual at higher elevations (Young et al., 1969), limiting recruits to more favorable weather conditions in the spring. Downy brome that germinates in the fall through early spring occupies an open niche, exploiting moisture and nutrients throughout the winter and early spring when most other desirable co-occurring species are dormant. Early-season utilization of soil moisture and nutrients allows downy brome to displace native grass, forb, and shrub species (Young et al., 1969; Thill et al., 1984; DiTomaso et al., 2010). If land managers fail to manage the downy brome soil seed bank, further invasions and reestablishment are likely to occur.

Long-term downy brome control might seem nearly impossible, but a number of researchers have identified a key aspect of downy brome biology that could provide the basis for long-term management: seed viability and seed longevity. Studies have shown a high percentage (96%−99%) of first-year downy brome seeds germinate the fall following addition to the soil seed bank (Burnside et al., 1996), with few persisting more than 2 yr in the soil (Haferkamp et al., 2001; Smith et al., 2008). Other studies have found that there was no persistence in the soil seed bank after 5 yr (Thill et al., 1984; Burnside et al., 1996). Studies conducted by Andersen et al. (1992) and Hewlett et al.

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http://dx.doi.org/10.1016/j.rama.2016.12.003

(1981) showed that downy brome management of > 2 yr is necessary to deplete the soil seed bank. Manipulating the soil seed bank may hold considerable promise for long-term downy brome management.

Managing downy brome with herbicides to enhance native grass establishment is not a new concept. Many of the same concerns about the loss of sagebrush ecosystems were articulated in the 1960s and 1970s, surprisingly for the same reasons described in 2014 (Chambers et al., 2014). Previous reports described the use of atrazine and paraquat to manage downy brome infestations and enhance native grass establishment (Eckert and Evans, 1967; Evans et al., 1967). Newer herbicides are available, but provide limited residual downy brome control. Integrating prescribed burning with herbicides (Kyser et al., 2007; Sheley et al., 2007; Davies and Sheley, 2011; Calo et al., 2012; Kessler et al., 2015) and targeted grazing (Diamond et al., 2012) have provided some increase in the length of downy brome control, but not to the extent necessary to deplete the soil seed bank (Cummings et al., 2007).

A recent publication describing a new herbicide for winter annual grass control suggested if downy brome was controlled for 4 − 5 yr, the soil seed bank could be depleted (Sebastian et al., 2016). Multiple reports suggest the longevity of downy brome seed in the soil is < 5 yr (Young et al., 1969; Burnside et al., 1996; Smith et al., 2008). Therefore, it may be possible to eliminate downy brome by managing seed production with herbicides alone or in combination with prescribed burning or other management practices (Smith et al., 2008; Diamond et al., 2012; Kessler et al., 2015; Sebastian et al., 2016).

The objective of this research was to test the hypothesis that eliminating downy brome seed production for multiple seasons could deplete the soil seed bank. This research was conducted at two locations in Colorado that were severely impacted by downy brome, but still retained some native vegetation.

Methods

Site Description

In 2010 field experiments were established at two downy brome − infested sites that were approximately 40 km apart. Site 1 (lat 40°28'2.58"N, long 105°9'13.40"W, 1 670-m elevation) is located near Loveland, Colorado on Devil's Backbone Open Space property (~890 ha) and is designated as a priority conservation area. Site 2 (lat 40°42'38.12"N, long 104°51'53.02"W, 1 640-m elevation) is located near Nunn, Colorado on a State Wildlife area that had previously been taken out of crop production. Both sites are located on the western edge of the central shortgrass prairie and are dominated by western wheatgrass *(Pascopyrum smithii)*, green needlegrass *(Stipa viridula)*, blue grama *(Bouteloua gracilis)*, and sand dropseed *(Sporobolus cryptandrus)*.

To determine soil characteristics at each site, three 10-cm-deep soil cores were taken in each of the four replications. These soil cores were combined into a composite soil sample and analyzed at the Colorado State University Soil Testing Laboratory. Site 1 has shallow, well-drained soils in the Ratake series (sandy loam, loamy-skeletal, micaceous, frigid, shallow Typic Haplustolls) with 2.5% organic matter, and Site 2 has deep, well-drained soils in the Nunn series (sandy clay loam, fine, smectitic, mesic Aridic Argiustolls) with 2.0% organic matter (USDA-NRCS, 2014).

Mean annual precipitation based on the 30-yr average (1981 − 2010) was 420 mm at Site 1 and 361 mm at Site 2 (Western Regional Climate Center, 2013). Precipitation across both sites was close to the 30-yr average in 2010 and 2011. A statewide drought occurred in 2012 with average total precipitation for both sites decreasing 160 mm below their 30-yr averages. In 2013, Site 1 received an additional 174 mm above the 30-yr average, while Site 2 had average precipitation. Both sites received an additional 58 and 76 mm of precipitation above their 30-yr averages in 2014 and 2015, respectively (CoCoRaHS, 2015). The mean annual temperatures ranged from 8.7 to 8.9°C, and during the years of this study temperatures were close to average.

Before herbicide applications, visual percent canopy cover was estimated by a team of experienced rangeland specialists, across the entire study area for all species present at both locations. Site 1 was characterized by ~90% downy brome canopy cover with a dense litter layer (2 − 7 cm) and scattered perennial grasses including western wheatgrass, blue grama, and sand dropseed (8% ± 3% [mean ± SE], 15% ± 4%, and 9% ± 4% canopy cover, respectively). Site 2 had less downy brome canopy cover before herbicide application (~70% cover) and several desirable species, including western wheatgrass, sand dropseed, and green needlegrass (13% ± 5%, 6 ± 1%, and 3% ± 1% canopy cover, respectively).

Experimental Design and Evaluations

Field Study

We applied glyphosate to 6 x 9 m plots in late spring (between 15 and 29 March) after annual grass emergence, to eliminate downy brome seed production for periods ranging from 0 to 5 consecutive yr (2011 − 2015). At the time of application, all perennial grasses were considered dormant. Six herbicide treatments, including a nontreated control, were arranged in a randomized complete block design with four replications. All treatments were applied with a CO_2-pressurized backpack sprayer using 11002LP flat fan nozzles calibrated to deliver 187 $L \cdot ha^{-1}$. Glyphosate (Roundup Weathermax, Monsanto, 1.26 $kg \cdot ae \cdot ha^{-1}$) plus adjuvant (methylated seed oil, MSO Concentrate with LECI-TECH, Loveland Products, 1.17 $L \cdot ha^{-1}$) was applied for 0, 1, 2, 3, 4, or 5 consecutive yr. The high glyphosate rate in this study was used to ensure complete downy brome control at this late spring timing.

Biomass Harvest

Biomass harvests were conducted in August (2011 − 2015) to evaluate compositional changes in the plant community in response to sequential glyphosate applications. Aboveground biomass of the downy brome and perennial grasses were harvested from randomly placed 1-m^2 quadrats. One quadrat was harvested per plot per year at each site ($n = 24$ per site). Harvested quadrats were not taken from the same location in the plot in consecutive years. Perennial grasses were separated by species during harvest. The material was dried at 60°C for 7 d to determine species dry biomass for each quadrat.

Greenhouse Soil Cores

To evaluate the yearly variation and depletion of the downy brome soil seed bank in response to consecutive glyphosate applications (0 − 5 yr), soil cores were obtained annually in March before herbicide application. Baseline cores were taken in March 2011 at initiation of the study, and final cores were taken in January 2016. Soil was collected from random locations within each plot (6 total cores per plot) using 3.8 cm deep x 5.1 cm diameter soil cores. Downy brome seedlings that had already emerged in the field during soil core collection were counted and added to the final downy brome total for the entire plot. The six soil cores from each plot were combined into one composite sample and immediately frozen at -20°C until greenhouse planting. Approximately 5 mo after collection, composite soil samples were spread uniformly over 25 x 25 x 6 cm flats arranged in a completely randomized designed. Flats were kept at field capacity with a 15-hr photoperiod to promote germination of all viable seeds. We allowed ~3 wk for all seedlings to germinate before conducting downy brome and perennial grass seedling counts to determine germination across sequential glyphosate treatments as compared with nontreated controls. Downy brome seedlings counted in March and greenhouse germinated seedlings from soil cores were pooled into a single value representing the viable downy brome seed in each treatment.

Statistical Analysis

Biomass Harvest

We used a repeated measures (PROC GLIMMIX) in SAS 9.3 to analyze downy brome field biomass harvest data (SAS Institute, 2010). Factors included in the repeated measures model were experiment, treatment, year, and all possible interactions, with year as the repeated measure. Dry biomass data were converted to a percentage by comparing treated with nontreated plots to normalize data variations in overall downy brome and perennial grass biomass across sites and years. These percentages were arcsine square root transformed, and a Tukey-Kramer adjustment was applied. After failing to reject the null hypothesis of equal variance for the repeated experiment ($P = 0.452$), the same residual variance was assumed and data were combined across sites for analysis. Differences among least squares means were analyzed across all 5 yr to evaluate the significant treatment-by-year interaction ($P < 0.0001$).

The biomass harvest conducted the last year of the study (6 August 2015) provided a final downy brome and perennial grass evaluation. Four-parameter logistic regression of dry biomass was conducted in Graphpad Prism 6 using the model:

$$Y = C + \frac{(D - C)}{1 + 10^{(LogGR_{50} - X) \cdot b}} \tag{1}$$

Where C is the lower limit of response, D is the upper limit of response, b the slope, and GR_{50} is the herbicide rate resulting in 50% reduction in biomass. Analysis was performed separately at each site for downy brome and perennial grass biomass because of unequal variances ($P < 0.0001$ and $P = 0.0063$, respectively).

Canopy Cover Estimates

Following the final treatment year, percent canopy cover estimates were also conducted in August 2015 for all perennial grasses. Canopy cover was determined by comparing visual estimates of downy brome canopy cover in the treated compared with nontreated plots using the whole 6 x 9 m plot area. All warm and cool season species were evaluated separately at each site. After failing to reject the null hypothesis of equal variance for the repeated experiment, the same residual variance was assumed and data were combined across sites for analysis of variance.

Greenhouse Soil Cores

Soil cores were analyzed to estimate the longevity of the downy brome soil seed bank. Because soil cores were collected in March (2011 − 2016) before treatments were applied, emerged seedlings were included in the total seedling counts for each treatment. Seedling counts were summed for each plot by combining emerged downy brome seedling counts made during collection of soil cores from the field (6 cores/plot), with seedling counts from the soil core greenhouse bioassay. These total counts were representative of the downy brome emerging as seedlings before the yearly glyphosate treatments and those remaining in the soil seed reserve after treatment. Total seedling counts were converted to a percent of the nontreated controls and analyzed in SAS 9.3. Data were arcsine square root transformed, and least squares means were analyzed using repeated measures as previously described. After failing to reject the null hypothesis of equal variance for the repeated experiment, the same residual variance was assumed and data were combined for analysis.

Results

Field Biomass

Based on the evaluation of the significant treatment-by-year interaction ($P < 0.0001$) and pairwise comparisons of least squares means ($\alpha = 0.05$), 1 − 3 yr of consecutive glyphosate applications were insufficient to deplete the downy brome soil seed bank (Fig. 1). Although treatment comparisons showed downy brome biomass was significantly reduced after glyphosate applications up to 3 consecutive yr, downy brome biomass and the soil seed bank recovered within 1 − 2 yr after applications were terminated ($P > 0.05$) (see Fig. 1). Treatments with 4 and 5 consecutive yr of glyphosate were necessary to eliminate the downy brome seed rain, while also depleting all viable downy brome seed in the soil seed bank (see Fig. 1). In yr 5, downy brome reestablished completely in treatments of 1 − 3 yr of glyphosate applications as compared with 4 and 5 yr of soil seed bank management ($P < 0.0001$).

The biomass harvest in the final year of our study (2015) showed a similar trend in downy brome biomass reduction compared with the yearly biomass harvests. Applying glyphosate to control downy brome biomass and seed production for 1, 2, and 3 consecutive yr resulted in similar downy brome biomass to the control (no herbicide treatment) ($P = 0.285 - 0.700$); however, eliminating downy brome seed production for 4 and 5 yr using glyphosate was effective in managing the downy brome soil seed bank as reflected by downy brome biomass (Fig. 2) ($P < 0.0001$). Compared with the nontreated control plots, perennial grass biomass remained fairly stable with 1, 2, and 3 yr of consecutive glyphosate applications compared with the nontreated ($P = 0.145 - 0.850$) (see Fig. 2). Eliminating downy brome competition with 4 consecutive yr of glyphosate resulted in a 4-fold increase in perennial grass biomass for sites 1 and 2, respectively ($P = 0.040$ and 0.019, respectively), while 5 yr of consecutive glyphosate applications resulted in a 7- and 9-fold increase in perennial grass biomass at sites 1 and 2 compared with the nontreated, respectively ($P = 0.001$ and 0.0002, respectively) (see Fig. 2).

Eliminating downy brome competition and seed production for 5 yr using glyphosate significantly increased perennial grass canopy cover approximately 2.9- and 1.6-fold as compared with the nontreated at sites 1 and 2, respectively (Table 1) ($P = 0.0011$ and $P = 0.0004$, respectively). Although perennial grass biomass increased significantly with 4 yr of consecutive glyphosate applications at sites 1 and 2 (see Table 1, $P = 0.006$ and 0.001, respectively), percent canopy cover estimates of all perennial grass (August 2015) showed a shift in the native plant community (Fig. 3). The plant community shifted from a cool season to primarily a warm season grass-dominated plant community (see Fig. 3). In order to control all the emerged downy brome with a single herbicide application, it was necessary to wait as long as possible in the spring. It is possible that the cool season grasses were not completely dormant when glyphosate was applied and the stress association

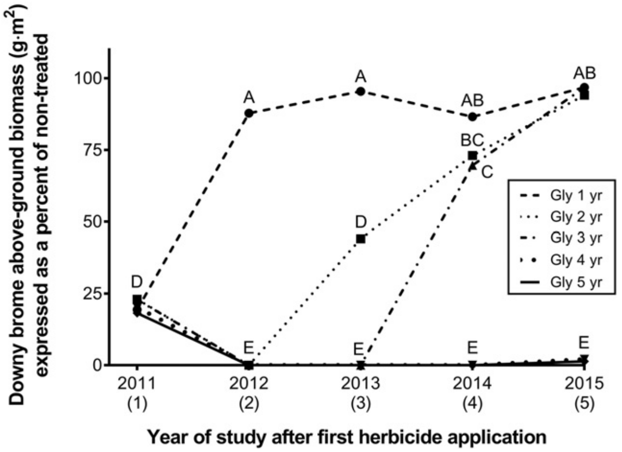

Figure 1. Effects of sequential annual glyphosate applications at sites 1 and 2 on downy brome biomass represented as a percent of the nontreated. Lines signify treatments with different levels of sequential glyphosate applications (Gly, 1.26 kg·ae·ha^{-1}). Letters indicate differences in least squares means across years ($P < 0.05$).

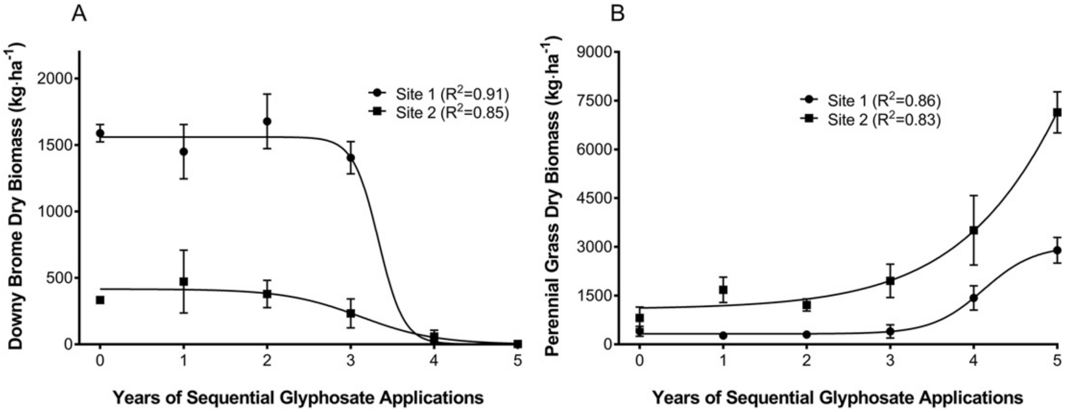

Figure 2. Four-parameter logistic regression evaluating the effects of sequential glyphosate applications on **A,** downy brome and **B,** perennial grass biomass. Data presented are from the August 2015 final biomass harvest. Point estimates ± SE represent differences in biomass across treatments.

with the herbicide treatments was responsible for shifting the plant community to one dominated by warm season grasses.

Applying high rates of glyphosate in the late spring poses a risk and would not be a recommended practice; however, it represented the best option for complete downy brome control with a single herbicide treatment. This project was intended to explore the importance of the soil seed bank as a key component in maintaining downy brome populations at levels that cause significant ecological impacts.

Greenhouse Soil Core Bioassay

Seedling counts made in the field and seedlings that established from soil cores in the greenhouse showed a similar trend to the yearly biomass harvests (see Figs. 1 and 4). Baseline soil cores collected in 2011 before herbicide treatments were initiated showed no difference among downy brome seedling counts across the sites (see Fig. 4, $P > 0.05$). One yr of glyphosate resulted in a 60% reduction in seedling germination from the soil seed bank compared with the nontreated plot; however, if glyphosate treatments were terminated, downy brome seedling counts recovered to baseline levels within 2 yr (2014) ($P = 0.355$). This same trend was consistent with 2 and 3 consecutive yr of glyphosate treatments. After glyphosate treatments were terminated, it took approximately 2 − 3 yr for the downy brome soil seed bank to recover to the level of the nontreated plots (see Fig. 4) ($P > 0.416$).

In 2015, plots where downy brome biomass and seed production were eliminated for 4 and 5 yr using glyphosate, downy brome seedling counts were 1% and 0% compared with the nontreated plots, and in 2016 seedling counts were 4% and 0% compared with the nontreated plots, respectively (see Fig. 4). By 2016, the soil seed bank for all other treatments had recovered to levels similar to the nontreated controls ($P > 0.979$), suggesting that > 3 yr of effective management is required to exhaust the downy brome soil seed bank (Fig. 5). Final soil core results in 2016 suggest that compared to 1, 2, and 3 yr of glyphosate, 4 and 5 yr of consecutive glyphosate application were critical to prevent downy brome reestablishment via the soil seed bank (see Fig. 5) ($P < 0.0001$). Interestingly, downy brome emergence from soil cores in the greenhouse showed no perennial grass seedling emergence in the treatments with 0 − 3 yr of glyphosate; however, soil cores taken from sites 1 and 2 with 4 yr of consecutive applications had on average 1 584 ± 336 (mean ± SE) and 1 120 ± 480 perennial grass seedlings per m^2, respectively. Perennial grass seedling counts further increased with 5 yr of glyphosate applications at both sites with an average of 2 528 ± 1 072 and 1 616 ± 848 seedlings per m^2, respectively.

Discussion

Our study provides evidence to support the hypothesis that the downy brome soil seed bank can be managed to a point of full control. Yearly field biomass harvests showed that at least 4 yr of consecutive control were required to maintain downy brome control, while at the same time depleting the soil seed bank. Management strategies that only provide 1 to 3 yr of control are susceptible to reestablishment from the soil seed bank. It is crucial when managing invasive winter annual grasses such as downy brome to consider the longevity of the seed

Table 1
Total perennial grass canopy cover in reponse to sequential glyphosate applications at sites 1 and 2. Visual percent canopy cover estimates (mean ± SE) were conducted August 2015 after the final year of herbicide applications.

Site	Sequential glyphosate applications (No.)	% Total perennial grass cover (Mean ± SE)
1	0	28.3 ± 14.1
1	1	17.3 ± 4.2
1	2	12.0 ± 2.6
1	3	21.0 ± 4.9
1	4	62.3 ± 8.3
1	5	80.8 ± 10.6
2	0	62.3 ± 10.0
2	1	60.6 ± 2.8
2	2	54.1 ± 5.3
2	3	69.3 ± 6.4
2	4	92.3 ± 3.8
2	5	98.8 ± 1.3

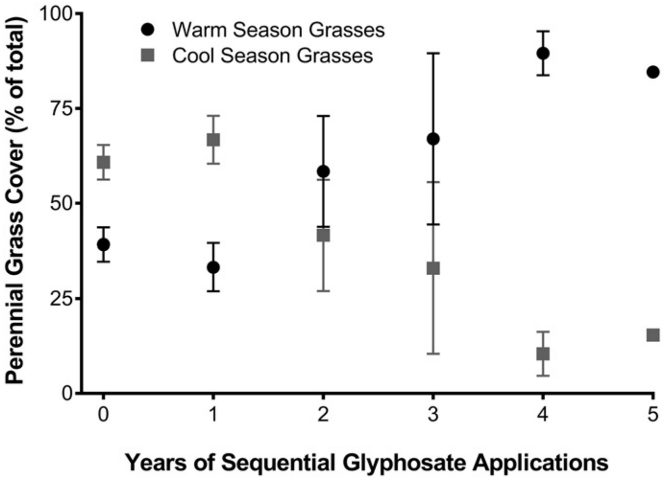

Figure 3. Perennial grass response (cool and warm season) to sequential glyphosate applications at two sites. Visual percent canopy cover estimates (mean ± SE) were conducted August 2015 after the final year of herbicide applications.

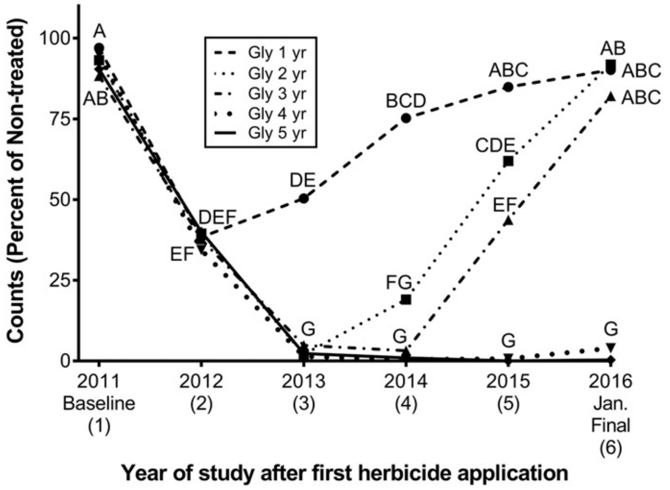

Figure 4. Determining the longevity of the downy brome soil seed bank using downy brome seedling emergence (counts) from soil cores taken in the field and germinated under optimum growing conditions in the greenhouse. Seedling counts were represented as a percentage compared with the nontreated. Lines signify treatments with different levels of sequential glyphosate applications. Letters indicate differences at $P < 0.05$.

in the soil seed bank. This may represent a trait that can be exploited to reduce the potential for reestablishment, and it is a trait shared by a number of other invasive winter annual grasses (Young, 1992; Burnside et al., 1996; Davies, 2008; Beck, 2009; Wallace et al., 2015).

Our data provide a framework for managing downy brome with a multiyear approach. It has been common for land managers to use herbicides, prescribed burning, or targeted grazing for a single growing season, where follow-up treatments or sequential herbicide applications are not made. Commonly recommended herbicides such as imazapic, glyphosate, or rimsulfuron provide limited or no residual downy brome control past the initial application year and can injure co-occurring species (Baker et al., 2009; Morris et al., 2009; Hirsch et al., 2012; Brisbin et al., 2013; Kyser et al., 2013; Mangold et al., 2013; Ehlert et al., 2015; Espeland and Kilian, 2015; Sebastian et al., 2016). Without long-term management of the soil seed bank, sites with downy brome will rapidly reestablish and return to nontreated plant densities within 1 – 2 yr (see Fig. 1) (Humphrey and Schupp, 2001; Allen et al., 2008).

The results from the current study suggest that land managers have two main herbicide approaches for depleting the soil seed bank in an attempt to restore downy brome – invaded rangeland. These include 1) annual applications of a herbicide such as glyphosate with limited residual downy brome control or 2) apply a herbicide with residual control every other year. A herbicide that provides extended downy brome control is necessary to exhaust the soil seed bank; however, there are limited herbicides that can provide this residual control. Land managers could use this framework to plan sequential applications like the methods used in this study, to control the downy brome crop for the 4 and 5 yr necessary to deplete the downy brome seed bank.

Indaziflam (Esplanade, Bayer CropScience) offers a new mode of action to noncropland weed management that provides up to 3 yr of residual downy brome and feral rye (*Secale cereale* L.) control with a single application (Sebastian et al., 2014; Sebastian et al., 2016). Using an indaziflam treatment the first year with our approach has the potential to provide residual control for 2 – 3 yr, requiring only one additional treatment to exceed the 3-yr downy brome seed bank threshold. Reducing herbicide applications from annual to once every 2 – 3 yr may minimize nontarget impacts to the desirable plant community, decrease labor costs, and decrease selection pressure for herbicide resistance. In contrast, the application of sequential glyphosate in late spring may also result in shifts in native species compositions over time (Rodney

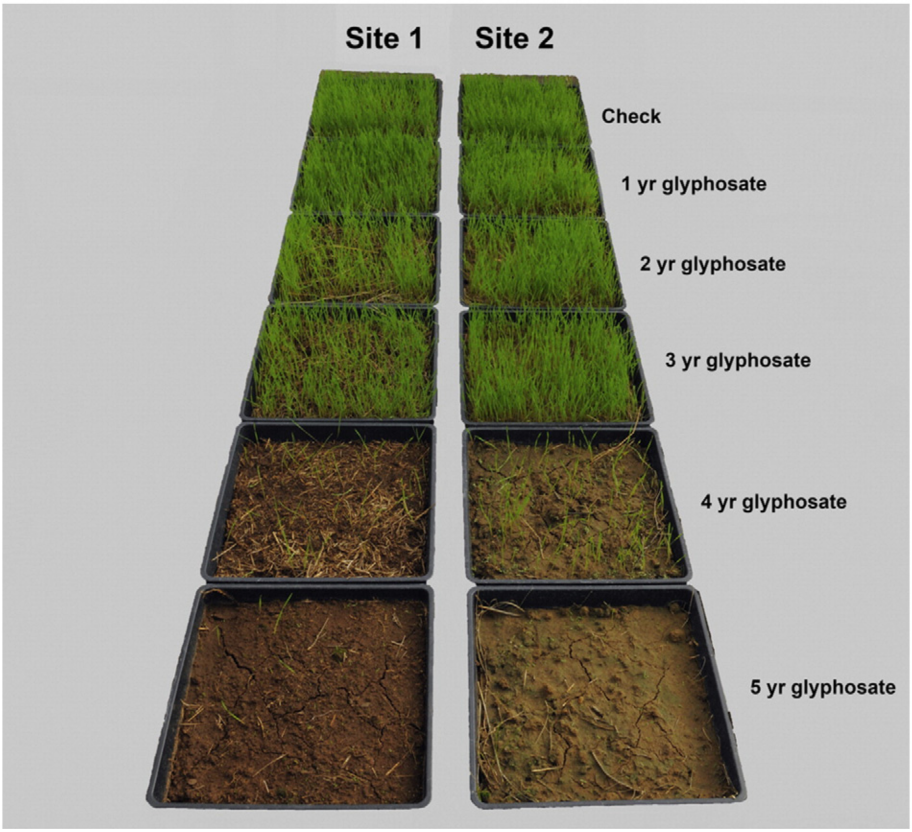

Figure 5. Soil cores collected January 2016 at sites 1 and 2, demonstrating the longevity of the downy brome soil seed bank in response to sequential glyphosate applications.

and Donald, 1991; Whitson et al., 1997). Indaziflam could provide an alternative strategy for land managers to treat downy brome for long-term control while also minimizing negative impacts to the desirable plant community (Sebastian and Nissen, 2016; Sebastian et al., 2016).

Long-term management of downy brome and the soil seed bank could be an important strategy to restore rangeland infested with downy brome and other annual grasses, particularly within the sage-steppe ecosystem (Crawford et al., 2004; USFWS, 2015). Among the 350 species that call the sage-steppe ecosystem home, the greater sage-grouse is one species in particular that has been directly impacted by large-scale downy brome invasions (Crawford et al., 2004; Baker et al., 2009; USFWS, 2015). According to a Department of the Interior news release, Secretarial Order 3336 (5 January 2015), reducing downy brome impacts is vital to sagebrush landscapes and productive rangelands (USFWS, 2015). Managing downy brome and its soil seed bank is imperative to create large-scale fire breaks and large blocks of high-quality sagebrush habitat needed for the many species that use the sage-steppe (Chambers et al., 2014). Collaboration between federal and state agencies (70% of sagebrush habitat) will be critical to address annual grass invasions (USFWS, 2015).

Implications

Downy brome invasions are rapidly transforming perennial plant communities into annual grass-dominated communities (Young and Longland, 1996), with an average annual spread rate of 14% (Duncan et al., 2004). Restoring the structure and function of these invaded ecosystems can be accomplished by targeting these invasive annual grasses; however, long-term control options are limited. Many factors can lead to the success or failure of downy brome control, and our research suggests that one major factor to consider is the longevity of downy brome seeds in the soil seed bank. Managing the downy brome seed bank targets a fundamental biological and ecological survival mechanism of this invasive weed. Our study provides much-needed evidence for why reestablishment via the soil seed bank occurs when using short-term downy brome control methods such as herbicides (glyphosate, imazapic, or rimsulfuron), prescribed burning, or targeted grazing. These control methods are commonly recommended, yet they have provided limited residual activity (Morris et al., 2009; Hirsch et al., 2012; Kyser et al., 2013; Mangold et al., 2013) and inconsistent long-term control (Diamond et al., 2012). We suggest eliminating downy brome seed production for > 3 yr provides the time needed to deplete the downy brome soil seed bank and significantly increase desirable perennial grass biomass and cover.

We recommend land managers recognize the importance of managing the downy brome soil bank and develop a multiyear plan to combat invasive winter annual grasses. Products such as indaziflam with residual control may provide an effective tool for invasive winter annual grass control that could be used in alternate years reducing the amount of total herbicide applied. Otherwise, managers could choose to apply herbicides with shorter residual control (e.g., glyphosate, imazapic, rimsulfuron) yearly until the soil seed bank is depleted (~3 yr). We caution managers to evaluate potential impacts to native seed banks and existing desirable flora before any application.

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