



Original Research

Downy Brome Control and Impacts on Perennial Grass Abundance: A Systematic Review Spanning 64 Years[☆]Thomas A. Monaco^{a,*}, Jane M. Mangold^b, Brian A. Mealor^c, Rachel D. Mealor^d, Cynthia S. Brown^e^a Ecologist, US Department of Agriculture (USDA)—Agricultural Research Service (ARS), Forage and Range Research Laboratory, Utah State University, Logan, UT 84322, USA^b Associate Professor and Extension Invasive Plant Specialist, Land Resources and Environmental Sciences Department, Montana State University, Bozeman, MT 59717, USA^c Director and Associate Professor, Sheridan Research and Extension Center, Sheridan, WY 82801, USA^d Extension Range Specialist, Ecosystem Science and Management Department, University of Wyoming, Laramie, WY 82071, USA^e Associate Professor, Bioagricultural Sciences and Pest Management Department, Colorado State University, Fort Collins, CO 80523, USA

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ABSTRACT

Given the high cost of restoration and the underlying assumption that reducing annual grass abundance is a necessary precursor to rangeland restoration in the Intermountain West, United States, we sought to identify limitations and strengths of annual grass control methods and refine future management strategies. We systematically reviewed all published journal articles spanning a 64-yr period (1948–2012; $n = 119$) reporting data on research efforts to either directly or indirectly reduce the abundance of the most common invasive annual grass, downy brome (*Bromus tectorum* L.). The seven most common control methods studied were herbicide, burning, revegetation, woody removal, defoliation or grazing, soil disturbance, and soil amendment. In addition, the majority of control methods were 1) applied at scales of 10–100 m², 2) sampled within small plots (i.e., 0.1–1.0 m²), 3) implemented only once, and 4) monitored at time scales that rarely exceeded 5 yr. We also performed summary analyses to assess how these control methods affect downy brome and perennial grass abundance (i.e., cover, density, biomass). We found conflicting evidence regarding the assumption that reducing downy brome abundance is necessary to enhance the growth and establishment of perennial grasses. All methods, with the exception of woody plant removal, significantly reduced downy brome in the short term, but downy brome abundance generally increased over time and only herbicide and revegetation remained reduced in the long term. Only burning, herbicide, and soil disturbance led to long-term increases in perennial grass abundance. We suggest that future research should prioritize a broader array of ecological processes to improve control efficacy and promote the reestablishment of desirable rangeland plant communities.

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Introduction

Degradation of dryland plant communities by exotic annual grasses is now recognized as a major driver of global environmental change (Ravi et al. 2009). Annual grass invasion transforms perennial grasslands and desert shrublands, resulting in drastic changes to perennial grass abundance, disturbance regimes, and ecological processes (Seastedt and Pysek 2011). Perhaps the most striking example is illustrated by shrubland and steppe ecosystems of western North America, where downy brome (*Bromus tectorum* L.) is spreading at an alarming rate (Duncan et al. 2004) and is the dominant vegetation on > 2 million ha (Bradley

and Mustard 2005). Its spread is a consequence of many interacting factors (Chambers et al. 2014a; Reisner et al. 2013), and when environmental conditions are altered to match predicted climate scenarios (i.e., warming; Bradley 2009), downy brome growth, reproductive output, survival, and phenology shift to favor invasion (Campagnoni and Adler 2014; Zelikova et al. 2013). Consequently, it is spreading to regions where it has not been abundant in the past, including the central and northern Rocky Mountains, southwestern forests, and the northern Great Plains (Bromberg et al. 2011; Douglas et al. 1990; Fowler et al. 2008; Mealor et al. 2012; Pawlak et al. 2015). This trend suggests that control and restoration strategies are keeping pace with neither downy brome rate of spread nor our breadth of ecological understanding of the causes of downy brome invasion and the conditions required to initiate ecosystem recovery (Chambers et al. 2014a; Reisner et al. 2013).

Our understanding of the causes of downy brome invasion rests on > 60 yr of research that reveals a dynamic interaction between disturbance and adaptive traits of the annual grass growth form. As summarized by Mack (1981), downy brome arrived to a region with inferior native plant competitors and to ecosystems that had undergone

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significant modification. In particular, disturbances during settlement in the mid-19th century in the form of clearing land for crops, unrestrained burning, and unregulated livestock grazing (Daubenmire 1940; Hull and Pechanec 1947; Morris et al. 2011; Pickford 1932) created ample opportunities for downy brome to invade where native herbaceous vegetation and biological soil crusts had been removed or severely impaired (Klemmedson and Smith 1964; Mack 1981; Turner 1971). Its long-term persistence and continued spread suggest that it has breached most barriers to invasion during its residency in western North America (Blackburn et al. 2011; Hastings et al. 2007; Hulme 2006).

Because downy brome invasion is associated with displaced native species (Arkle et al. 2014), altered fire regimes, and modified hydrological and soil properties (Blank and Morgan 2013; Davies et al. 2011; Wilcox et al. 2012), impacted ecosystems may not recover by simply removing the invasive grass. Removal may improve ecosystem functioning and the provisioning of services for less-impacted, low-level invasions. However, it is generally understood that highly altered rangeland sites with compromised ecosystem attributes (e.g., biological soil crusts, perennial grasses, and big sagebrush species [*Artemisia tridentata* Nutt.]) (Chambers et al. 2014a; Peterson 2013) can potentially remain in an alternative vegetation state characterized by poor restoration potential (Sheley and James 2014), frequent fires, and exotic species dominance (Young and Evans 1978; Allen and Knight 1984; Knapp 1992; Prev y et al. 2010; but see Bagchi et al. 2013). Consequently, control efforts must adequately address underlying conditions that favor downy brome dominance (Reisner et al. 2013; Sheley et al. 2010; Wisdom and Chambers 2009). Because downy brome invasion alters the abundance of perennial grasses and their ability to naturally recover following disturbance (Bagchi et al. 2013; Mata-Gonzalez et al. 2007), the manner in which they respond to control methods is also a critical aspect of rangeland management. For example, moderate levels of perennial grass cover equate to appreciable invasion resistance (Anderson and Inouye 2001; Davies 2011; Davies et al. 2010). Furthermore, increasing perennial grasses is considered necessary to initiate recovery toward a system where no further restoration treatments are necessary (Hirsch-Schantz et al. 2014; Nyamai et al. 2011).

Invasive plant management has been criticized for not considering how various control methods influence ecological processes associated with resistance to invasion and ecosystem resilience following disturbance (Brooks and Chambers 2011; Chambers et al. 2014a). Viewing invasive species removal in isolation can result in unexpected changes to other ecosystem components and unwanted secondary impacts (Zavaleta et al. 2001). It may also hamper the development of restoration goals (Buckley 2008; Firn et al. 2008; Hulme 2006; Tzankova and Concilio 2015). Consequently, there is a need to assess annual grass management in a broader ecosystem context to provide a clearer understanding of the strengths and weaknesses of various control methods (Buckley 2008; D'Antonio et al. 2004; Flory and Clay 2009). Fortunately, given the historical and ecological significance of downy brome invasion in western North America, a large body of research literature exists to systematically assess control methods and their impacts on perennial grass recovery. Such an assessment will improve dialogue among researchers and managers and make research results more instructive to practitioners seeking effective management solutions (Boyd and Svejcar 2009; Hulme 2011).

We systematically reviewed and quantitatively summarized the downy brome control literature that spanned > 60 yr. We sought to examine the relative efficacy of control methods, identify the disparities between past research and future downy brome management needs, and prioritize research topics to meet future management needs. We used published research articles to first define the spatial and temporal scales at which experimental treatments were applied and then contrast the impacts of control methods on downy brome and perennial grasses abundance (i.e., biomass, cover, and density). We asked two questions: 1) Do control methods effectively reduce downy brome abundance? and 2) Do control methods affect perennial grass abundance?

Methods

Literature Database

Research articles were assembled from Web of Knowledge (v. 5.9; Thomson Reuters, New York, NY), which accessed two primary databases: Web of Science (1975–2012) and CAB Abstracts (1910–2012). Using a *topic* search, we acquired citations for all articles that contained any of the following terms: downy brome, cheatgrass, *Bromus tectorum*, and downy chess. Of these ($n = 494$), we omitted articles that were not published in peer-reviewed journals or that did not include original data with downy brome as a response variable. We restricted our search to these criteria to ensure articles were easily accessible to readers.

Systematic Review

As a subset of the downy brome literature database, we identified articles for a systematic review and quantitative summary that met the following criteria: 1) reported original data from a field setting (i.e., we excluded greenhouse and laboratory experiments), 2) were conducted in a rangeland setting (i.e., excluded agricultural crop studies), 3) contained mean values for downy brome or perennial grasses abundance, and 4) directly compared an untreated control with at least one downy brome reduction treatment ($n = 119$; Appendix S1, available online at [doi:10.1016/j.rama.2016.09.008]). We sought to reveal as much relevant information about this body of research as possible by defining trends in article publication over time, patterns of study location, relative prevalence of control methods, occurrence of integrated/multiple control approaches, and contextual elements of studies including treatment plot size, sampling plot size, control period (e.g., method implementation period), and monitoring period. These metadata were recorded for each article and helped identify seven primary control methods: herbicide; burning (prescribed fire and wild-fire); revegetation (seeding of perennial grasses); woody plant removal (long-lived shrubs and woodland tree species); defoliation (mowing, grazing); soil disturbance (tillage, disking, and plowing applied before seeding perennial grasses); and soil amendments (adding labile carbon sources to increase microbial soil biomass and immobilize mineral nitrogen in soils and/or treatments to specifically reduce plant litter on soil surfaces). Although woody plant removal studies did not specifically target downy brome, we included them because treatments inadvertently influence downy brome abundance and were frequently applied with other control methods.

Quantitative Summary Analysis

To analyze how the seven control methods influence downy brome and perennial grass abundance, we calculated effect sizes, which are typically used to quantify the magnitude and direction of a treatment using meta-analysis. However, it was not possible to conduct a formal meta-analysis on our dataset because we could not perform the mandatory steps of weighting estimates of effect size by within-study variance for a large proportion of older studies (Vetter et al. 2013). Consequently, because our desire was to include data from all studies that met our criteria, we conducted a quantitative summary analysis of downy brome and woody plant control measures using effect size estimates that do not rely on within-study variance (Hedges et al. 1999). Recent reviews clearly distinguish between meta-analysis and quantitative summary analysis, and the latter does not strictly adhere to standardized meta-analysis methods (Harrison 2011; Koricheva and Gurevitch 2014; Vetter et al. 2013). Effect sizes were calculated as the natural log response ratio, $\ln(X_E/X_C)$, where X_E = treatment mean and X_C = control mean (Goldberg et al. 1999). We then pooled effect sizes and calculated mean effect sizes and 95% confidence intervals. Although this approach runs the risk of misrepresenting the true mean response of a control

method due to overemphasis of high-variability response ratios, we considered this risk minor compared with the biases introduced by excluding articles from the analysis because they did not report measures of variation (Gurevitch et al. 1992; Kettenring and Adams 2011; Koricheva and Gurevitch 2014). Positive effect sizes indicate an increase in a response variable (and vice versa for negative effect sizes), and the response magnitudes were considered significant if 95% confidence intervals did not overlap each other or zero.

For suitable research articles, we extracted mean values from tables or estimated them from digital scans of figures using DataThief III Version 1.5 (Myers and Harms 2009). Specifically, we recorded three measures of downy brome and perennial grass abundance: percentage canopy or basal cover, plant density, and biomass production. Because studies typically applied more than one downy brome control method to numerous sites, multiple effect sizes could be acquired from the same article. In addition, when data were collected at the same location over time, we calculated effect sizes for the first census (hereafter short term) and the last census (hereafter long term). For articles that included only a single census, it was considered short term if data were collected within 1 yr after treatment; otherwise they were considered long term if data were collected in the second year after treatment or thereafter. Although we calculated only single-factor effect sizes, values from multi-factor experiments were also used. For example, a herbicide treatment could serve as the control for a herbicide + burn treatment to assess the effect of burning. We performed separate summary analyses for percent cover, density, and biomass by pooling responses for all control methods. We also performed separate summary analyses for the seven control methods by pooling abundance measures.

Results

Our initial literature search produced 494 unique articles that were published over 68 yr between 1944 and 2012. Of these, 119 were published from 1948 to 2012 (i.e., 64 yr) and met our criteria for consideration as control method articles (Table S1 in the online version at doi:10.1016/j.rama.2016.09.008). The cumulative number of downy brome research articles increased beginning in the 1990s and reached a maximum output of articles in 2010. In contrast, the number of control method articles remained below three per year until 2007, after which publication output sharply increased.

Study Locations

The 119 downy articles reported on studies conducted at 227 unique locations in western North America (Fig. 1). Nearly 90% of studies occurred within two Level II Ecoregions (<http://archive.epa.gov/wed/ecoregions/web/html/ecoregions-2.html>): Cold Deserts (50%) and the Western Cordillera (39%). We did not find published research articles reporting control efforts outside of North America that met our criteria.

Systematic Review

The most commonly studied methods in decreasing order were herbicide (55%), burning (29%), revegetation (29%), woody removal (21%), defoliation (16%), soil disturbance (13%), and soil amendment (8%). Most articles (55%) evaluated only one control method, followed by two-method combinations (38%). The most frequent two-method

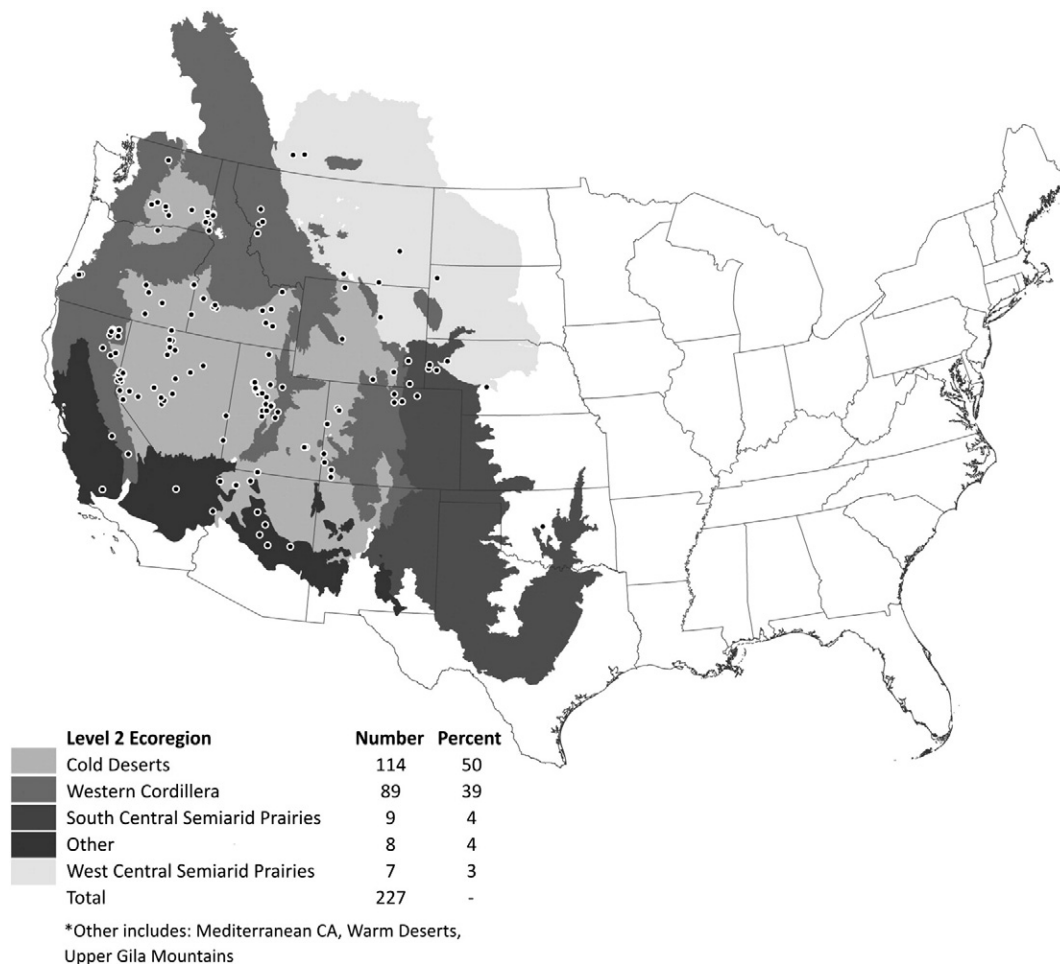


Figure 1. Locations of studies (points) included in the downy brome summary analysis overlaid on Level II Ecoregions with number of published studies and percent of total per ecoregion.

control combinations included either herbicide or revegetation. Herbicide was most frequently used with revegetation (9%) and woody removal (8%). In addition, revegetation was also most commonly applied with burning (8%).

A large percentage (64%) of articles reported studies where the treatment area was greater than 10 m²; the majority of studies treated an area between 10 and 100 m² (27%). In addition, several studies (17%) entailed large-scale wildfires or woody plant reduction efforts that did not specify treatment size. Similarly, a small number of studies (6%) used plot-less measures of plant abundance (e.g., line-intercept transects), or size was unspecified. Otherwise, most studies (78%) reported sampling plot sizes < 1 m². Overwhelmingly, most articles reported on control methods that were applied only once (87%), which were monitored for ≤ 5 yr (85%); 24% of studies were only monitored once. Studies monitored between 5 and 20 years (14%) were typically associated with assessing treatment effects many years after a large-scale prescribed fire or woody plant reduction effort.

Quantitative Summary Analysis

The 119 journal articles we reviewed yielded a high number of effect sizes for downy brome (1 258) and perennial grass (1 020) abundance. When effect sizes for the seven control methods were pooled, downy brome biomass, cover, and density were all significantly reduced in the short term (i.e., 95% confidence intervals did not overlap zero) (Fig. 2a). However, all three measures of downy brome abundance generally increased over the long term, yet only cover was > 0. Similarly, when the three measures of downy brome abundance were pooled, all control methods except woody plant removal resulted in reductions over the short term (Fig. 2b). Downy brome abundance also generally increased over the long term for all control methods, especially for burning and woody plant reduction methods, whose effect sizes were different than zero. Revegetation and herbicide were the only control methods to provide long-term reductions in downy brome abundance.

Effect sizes for all three measures of perennial grass abundance either increased or were not different than zero when the seven control methods were pooled (Fig. 3a). Perennial grass density increased initially after downy brome control, yet this effect was not significant over the long term. In contrast, perennial grass biomass and cover

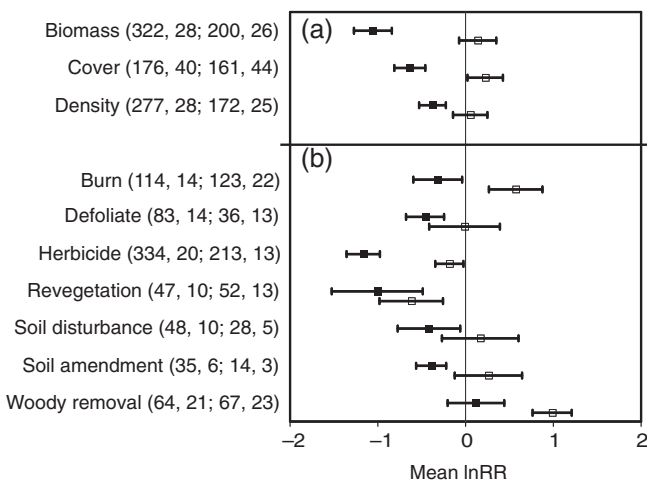


Figure 2. Results of summary analysis contrasting (a) three measures of downy brome abundance (control methods combined) and (b) seven control methods (abundance measures combined). Symbols represent mean effect sizes (log response ratios; lnRR ± 95% confidence intervals) 1 yr after treatment application (short term; solid) and ≥ 2 yr after treatment application (long term; open). Mean effect sizes are considered significant if confidence intervals do not overlap the vertical zero-line. Values in parentheses indicate sample sizes and the number of articles from which short- and long-term responses were acquired, respectively.

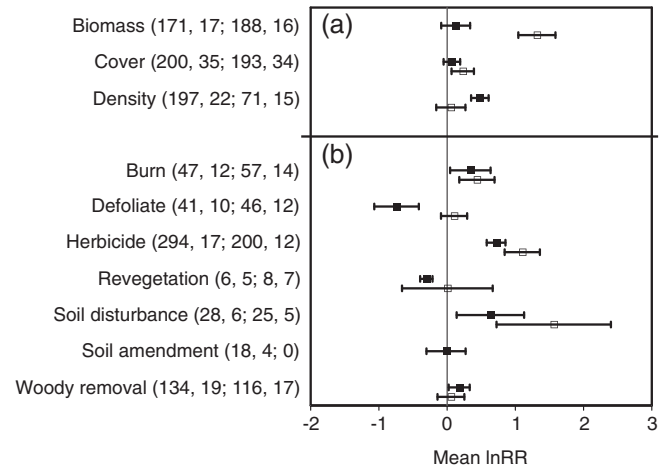


Figure 3. Results of summary analysis contrasting (a) three measures of perennial grass abundance (control methods combined) and (b) seven control methods (abundance measures combined). Symbols represent mean effect sizes (log response ratios; lnRR ± 95% confidence intervals) 1 yr after treatment application (short term; solid) and ≥ 2 yr after treatment application (long term; open). Mean effect sizes are considered significant if confidence intervals do not overlap the vertical zero-line. Values in parentheses indicate sample sizes and the number of articles from which short- and long-term responses were acquired, respectively.

were > 0 over the long term. Many control methods increased perennial grass abundance over the short term (Fig. 3b); however, only burning, herbicide, and soil disturbance resulted in long-term increases. None of the methods decreased perennial grass abundance over the long term.

Discussion

Our review revealed that past research emphasized how various control methods impact the abundance of downy brome and perennial plants. In addition, these methods were primarily applied only one time to areas < 1 ha. Moreover, much of this research was based on the assumption that reducing downy brome abundance is necessary to enhance the growth and establishment of perennial grasses (Stewart and Hull 1949; Evans 1961; Mack 2011). From our quantitative analysis of short- and long-term responses, we found conflicting evidence regarding this assumption. In support of this assumption, six of the seven methods reduced downy brome abundance, and three methods increased perennial grasses in the short term. In contrast, only one method, herbicide application, both decreased downy brome and increased perennial grass abundance over the long term.

The absence of lasting downy brome reduction and poor association between its reduction and perennial grass abundance suggest that future research will need considerable refinement. While past research provided a robust assessment of downy brome and perennial grass abundance via direct, “top-down” effects of control methods on plant mortality over the short term (< 2 yr), we suggest that future research should emphasize longer-term treatment applications and integrate a broader array of ecological processes when assessing control tools and strategies. To address the disparity between the past research focus and future research needs, we developed a simple conceptual diagram to emphasize the roles of additional processes in regulating downy brome and perennial grass coexistence (Fig. 4). This diagram is used to illustrate how downy brome management influences seven key ecological processes, as well as assist in identifying disparities between past research and future downy brome management needs.

Do Control Methods Effectively Reduce Downy Brome Abundance?

The post-treatment increase in downy brome abundance over time for most methods suggests that successful control will require

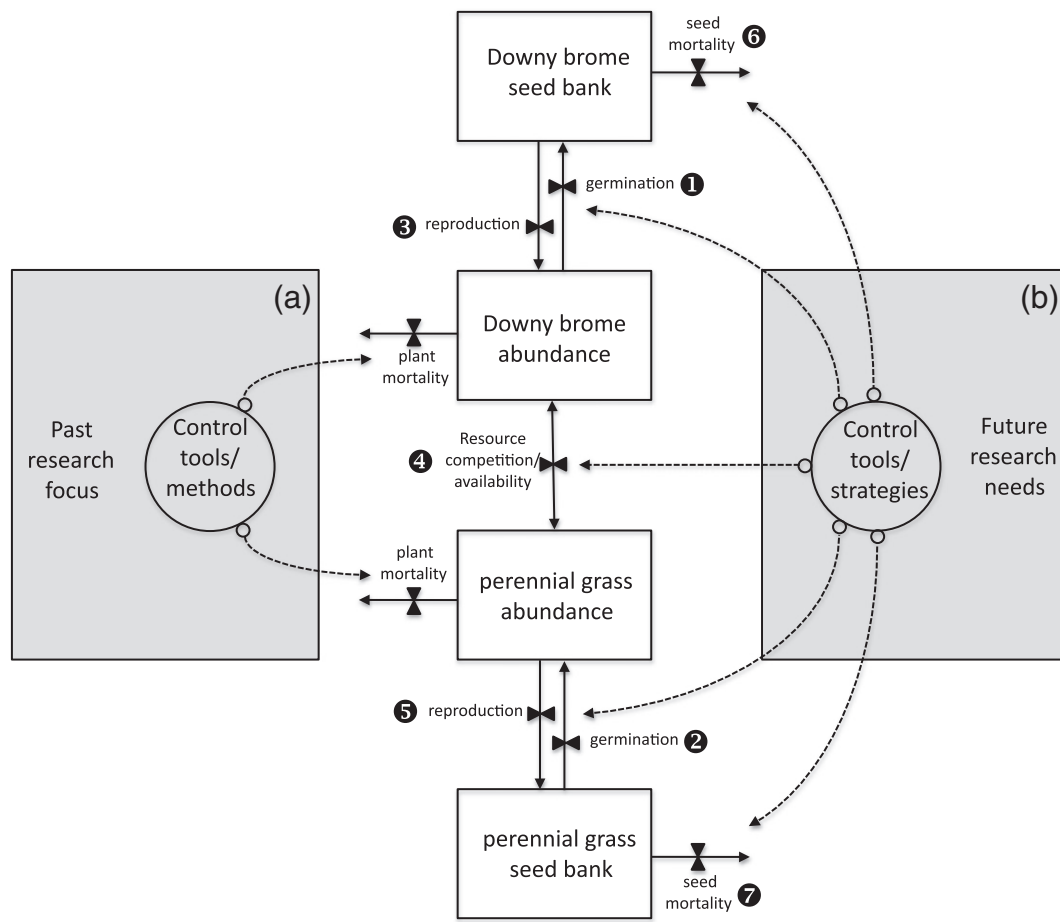


Figure 4. Conceptual diagram contrasting past research focus (a) and future research needs (b). In this diagram, control methods/strategies (large circles) are applied with the goal of impacting specific ecological processes (control valves), which in turn can influence the abundance of downy brome and perennial grasses (rectangles). On the basis of our systematic review, we conclude that past research is characterized by short-term studies that primarily applied control methods to reduce downy brome abundance by influencing plant mortality. In addition, we suggest that future research should explore how control methods impact a broader array of ecological processes in order to achieve greater longer-term restoration success.

considerable reductions in downy brome abundance over a long enough period in order for desirable resident species to recover or seeded species to successfully establish (Evans 1961; Rafferty and Young 2002). While this interpretation implies that reinvasion is likely the rule, herbicide and revegetation are exceptions, and their capacity to promote longer-term reductions in downy brome is likely related to residual effects on reproduction and germination processes (see Fig. 4, Points 1 and 3). For example, certain soil active herbicides are known to provide 2–3 yr of downy brome control by reducing propagule pressure (i.e., the number of individual plants dispersed and/or the number of dispersal events) and relative abundance within seed banks (Davison and Smith 2007; Elseroad and Rudd 2011; Hirsch et al. 2012). Similarly, yet through a different process (see Fig. 4, Point 2), revegetation provides residual control by impairing priority effects (i.e., the preferential establishment of downy brome due to earlier emergence). When perennial grass seedlings emerge before downy brome seedlings, they are more capable of competing for limiting soil water and nutrients and reducing downy brome abundance (Blackshaw 1993; Hull and Stewart 1948; McGlone et al. 2011; Orloff et al. 2013; Stevens and Fehmi 2011).

Research strategies that apply residual control over a longer-term control period with repeated applications are clearly needed for downy brome management (e.g., Jones et al. 2015; Munson et al. 2015), but demographic processes such as propagule pressure and priority effects are seldom prioritized in weed research (Davis 2006; Gallandt 2006; Reaser et al. 2008). Such research is critically needed because while downy brome seeds often germinate or die within 1 yr, a proportion of the seed bank does not germinate in the fall and winter of the first year or

can remain viable in the seed bank for up to 5 yr (Andersen et al. 1992; Hulbert 1955; Smith et al. 2008). Surviving seeds (i.e., caryopses) often remain in the soil or litter mass and are known to rapidly reestablish another stand (Brisbin et al. 2013; Hull and Hansen 1974; Morris et al. 2009). Consequently, delayed germination in downy brome (Dyer et al. 2012; Rice and Dyer 2001) is not only a strategy to buffer against poor years in variable or unpredictable environments (Braza and Garcia 2011; Brown and Venable 1986), but surviving seeds generate seedlings that interfere with the establishment of native perennial grass species (Rafferty and Young 2002; Young and Evans 1978). We also suggest that research emphasis needs to shift from merely reducing annual grass abundance to evaluating methods that impair priority effects and remediate short-term legacies left by annual grasses (Abraham et al. 2009; Corbin and D'Antonio 2004b; Grman and Suding 2010; Lulow 2006; Suding et al. 2004; Wainwright et al. 2012).

While herbicide and revegetation effectively reduced downy brome abundance, burning and woody plant removal increased downy brome abundance over the long term. These undesirable responses underscore the need for additional research that explores how methods affect downy brome reproduction, intraspecific competition, and resource availability (see Fig. 4, Points 3–4). For burning, the increase in downy brome abundance over time may be attributed to density-dependent effects on seed production (Lockwood et al. 2005; Warren et al. 2012). For example, downy brome plants that emerge after wildfires are typically larger, experience less intraspecific competition, and produce more seed relative to plants in unburned areas (Young and Evans 1978; Young et al. 1969). Low intraspecific competition provides a

plausible explanation for our observation of increased downy brome abundance in response to burning, even though abundance was significantly reduced in the short term, and in spite of equivalent increases in perennial grass abundance over the long-term. Consequently, control efforts can potentially perpetuate downy brome invasions to ecosystems even after perennial grasses become established. It may take a longer period than was monitored by the studies in our systematic review to assess how established perennial grasses effectively reduce downy brome. Accordingly, an assessment of postwildfire rangeland seedlings in the western United States showed lower abundance of invasive species, including downy brome, on sites where time since seeding was ≥ 3 yr compared with sites where time since seeding was < 3 yr (Pyke et al. 2013).

In contrast to burning, woody plant removal treatments resulted in increased downy brome abundance without significant changes in perennial grass abundance. This response is likely a consequence of disturbance-mediated impacts on soil resource availability and interspecific competitive interactions (Chambers et al. 2014a; Murphy and Romanuk 2012; Peterson 2013). When disturbances increase resource availability or decrease resource uptake by resident species, opportunities for exotic plant invasions are enhanced (Chambers et al. 2007; Davis et al. 2000; Hobbs and Hueneke 1992). Accordingly, it is well established that the growth and competitive ability of annual grasses are greatly increased by nutrient additions, which enables them to proliferate where the soil surface is disturbed (Adair et al. 2008; Cochran et al. 1990; Hobbs and Atkins 1988). Although woody plant removal did not intentionally target downy brome in the studies we assessed, these treatments often increase both annual grass abundance and soil resource availability (Bates et al. 2000; Blumenthal et al. 2006; Young et al. 2014). Woody plant reduction treatments are applied under the premise that removal of woody species will reduce their acquisition of soil resources and increase the relative abundance of herbaceous vegetation (Davies et al. 2012b; House et al. 2003; Ross et al. 2012). However, if understory vegetation is highly degraded, woody plant reduction may not yield desired outcomes (Davies et al. 2012a; Hess and Beck 2014). Alternatively, when desirable understory vegetation is still intact, and downy brome abundance is relatively low, woody plant removal can yield desired outcomes (Chambers et al. 2013; Pierson and Mack 1990; Whitson et al. 1988).

How Do Downy Brome Control Methods Affect Perennial Grass Abundance?

Although we did not confirm that downy brome control is required to enhance the establishment of perennial grasses, our analysis illustrates that burning, herbicide application, and soil disturbance simultaneously reduced annual grass abundance and increased perennial grass abundance in the short term. These results may be attributed to partial overlap in resource use and phenology between annual and perennial grasses (Borman et al. 1991; Hamilton et al. 1999) and subsequent interspecific competition for limiting resources (see Fig. 4, Point 4; Hull 1949; Leffler et al. 2013; Uselman et al. 2014). For example, treatments that reduce annual grasses increase soil water and mineral nitrogen availability for other species in the plant community (Adair et al. 2008; Hirsch-Schantz et al. 2014). Furthermore, the potential importance of competition among annual and perennial grasses has been illustrated across a wide range of rangeland sites, where their relative abundances are inversely related (Boyd and Davies 2012; Corbin and D'Antonio 2004a; Davies 2011; Gasch et al. 2013; Hamilton et al. 1999).

Strong competition between perennial grasses and downy brome is further demonstrated by Boyd and Svejcar (2011), who found that removing shrubs increased perennial grass abundance, while removing both perennial grasses and shrubs increased downy brome abundance between 3 and 10 yr after treatment. In our analysis, downy brome reduction appeared to stimulate early establishment of new perennial grass plants because only plant density increased significantly in the short term (see Fig. 3a). Downy brome reduction also appeared to

benefit the growth of existing perennial plants, however, as indicated by longer-term increases in both biomass and cover. In contrast, the short-term reductions in perennial grass abundance we observed with revegetation may be associated with mortality of preexisting perennial grasses in the first year after seeding. On the other hand, the fact that revegetation decreased cheatgrass but did not increase seeded grasses over the longer term (> 2 yr) may be related to the timeframe (i.e., 2–5 yr) when most seeding studies are evaluated, which may not be long enough for perennial grasses to reach a maximum abundance (Hardegee et al. 2016; Monaco et al. 2016). These results also imply that there is a narrow timeframe in which downy brome abundance is low and revegetation with perennial grasses is possible. Future research should focus on ways to capitalize on this narrow timeframe by seeding early-phenology perennial grasses that establish relatively quickly (Herron et al. 2013; Jones et al. 2010; Leger and Baughman 2014; Robertson and Pearse 1945) and addressing the establishment of later-successional species at some future date. In addition, continued research on the mechanism(s) responsible for perennial grass seeding failure or success is encouraged (see Fig. 4, Point 7; James et al. 2013; Robins et al. 2013), as well as studies to define how control methods influence soil and environmental microsite conditions to favor perennial grass establishment (Boyd and Davies 2010; Boyd and Van Acker 2004).

Maintaining the abundance of established perennial grasses through post-treatment management is an essential component of ecological restoration because vegetation dominated by perennial grasses has less variable annual net production and is typically more productive than downy brome in both dry and wet years (Bradley and Mustard 2005; Clinton et al. 2010; Klemmedson and Smith 1964). Enhancing a desirable balance between perennial grasses and downy brome, however, remains a challenge to land managers and more research is needed to better identify effective ways to maintain perennial grass abundance (Monaco et al. 2016). Previous studies suggest that perennial grass persistence depends on favorable reproduction and/or repeated sowing after establishment failures (see Fig. 4, Points 5 and 7), species capacity to withstand downy brome competition during the seedling establishment stage, and protecting established seedlings from excessive damage by livestock (Hardegee et al. 2011; Hironaka and Tisdale 1963; Knutson et al. 2014). For example, grazing mixed stands of native perennial grasses and downy brome may be detrimental to perennial grasses, which are favored by cattle (HilleRisLambers et al. 2010; Young et al. 1990). However, Bates and Davies (2014) found that 7 yr of cattle grazing at light and moderate levels after wildfire did not significantly alter cover, density, and production of resident perennial grasses or downy brome.

It is now generally recognized that high-resource availability favors the growth and spread of annual grasses (James et al. 2008; Lowe et al. 2003; Steers et al. 2011) and that resource availability strongly influences competition between native and non-native species (Abraham et al. 2009; Besaw et al. 2011; Kolb et al. 2002). For example, high soil resource availability has been correlated with downy brome abundance at the landscape scale (Brooks and Chambers 2011; Floyd et al. 2006; Hirsch-Schantz et al. 2014). Heavily invaded areas also have higher nitrogen availability, which perpetuates downy brome dominance of a site (Blank and Morgan 2013; Stark and Norton 2015). Research has shown that as downy brome abundance increases, resident native and seeded perennial species recruitment into the community will be limited due to downy brome exhausting limited soil moisture (Kulmatiski et al. 2006; Link et al. 1995; Melgoza et al. 1990). Given the importance of soil resource availability to downy brome abundance and the competitive outcome between annual and perennial grasses (Going et al. 2009; Johnson et al. 2011), future research in this area is clearly needed (see Fig. 4, Point 4).

Study Limitations

Although our effort is comprehensive of the published research literature over this 64-yr timeframe, there are three limitations to extrapolating

results to management applications. First, the majority of studies were conducted in ecoregions where downy brome has had long-term and large-scale impacts on plant communities (i.e., Great Basin) as opposed to regions where downy brome has a relatively shorter history of invasion (i.e., American Southwest, Pawlak et al. 2015). In addition, our analysis does not account for variation among biogeographic regions that are known to differ in disturbance and invasion history, as well as site resilience to environmental stress and disturbance (Bagchi et al. 2013; Bradley 2009; Brooks et al. 2016; Chambers et al. 2014a; Davies and Bates 2010). Second, the studies in our systematic review rarely applied a method more than one time. While short term, pulse-type experiments are a common method of evaluating control techniques in agricultural settings, they do not accurately represent how downy brome management programs are applied to private rangelands and federal lands where longer-term, adaptive management strategies are advocated (Leffler and Sheley 2012; Williams and Brown 2014). Third, the majority of studies used in our analysis (72%) applied control methods to areas < 1 ha, which is considerably smaller than areas typically treated in private and federal land management (Abella 2014; Hirsch-Schantz et al. 2014; Knutson et al. 2014). It is also possible that research plots may have been protected from continued disturbances like fire and grazing, thus providing a source of relief to recovering perennial grasses that would not occur in downy brome—invaded sites. Furthermore, discrepancy in spatial scale indicates that our results likely underestimate the range of variability in downy brome and perennial grass abundance across landscapes with greater spatial heterogeneity (Munson et al. 2015). However, these three limitations are common to systematic reviews of general invasive plant control, as well as in-depth assessments of individual invasive species (Hazelton et al. 2014; Kettenring and Adams 2011; Tyler et al. 2006).

Implications

On the basis of the results of our systematic review, we suggest two important downy brome control research needs: 1) Future studies should place greater emphasis on the ecological processes that can prevent reinvasion rather than only address the issue of annual grass control (Berger 1993; Buckley 2008; D'Antonio et al. 2004; Flory and Clay 2009), and 2) future studies should prioritize control tools and strategies that provide greater residual control of downy brome demographic processes (Bagchi et al. 2013; Chambers et al. 2014a; Lonsdale 1999). Because downy brome is a widespread invasive grass with long-term residency in some portions in western North America, it is doubtful that control efforts will result in its eradication; however, our review indicates that certain control efforts are capable of simultaneously decreasing downy brome while increasing perennial grass abundance. Special research attention should also be given to clarify situations where downy brome removal can have unintended negative consequences to the resident plant community (D'Antonio and Meyerson 2002; Meyer et al. 2014; Ratzlaff and Anderson 1995). For regions threatened by invasion, research efforts also must emphasize preventing introduction and fostering invasion resistance. Finally, our review strongly suggests that future research needs to minimize the discrepancy in scale between research and management by monitoring studies for longer timeframes (e.g., > 3 yr) while measuring how control methods impact plant communities and ecological processes at larger scales typical of land management on western US rangelands. In this vein, adapting control methods to larger, more heterogeneous rangelands is critically needed to better understand cross-scale responses to downy brome management activities (Monaco et al. 2016; Peterson et al. 1998).

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