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Summer water in a restored native grassland flushes annual grass seed bank but fails to increase native perennial cover

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Abstract. Natural and artificial flushing of the weed seed bank, followed by killing of seedlings, is a common practice in agricultural and prerestoration settings, but its application for post-restoration management has not been tested in the context of restored native plants. Summer watering at already restored sites could reduce exotic annual grass cover by decreasing the seed bank, thereby increasing native perennial success in subsequent growing seasons. Five replicated watering treatments of 11.35 L per watering event were applied for up to a 4 week period, with watering events ranging from once daily for a minimum or four and maximum of 16 d, or twice daily for 4 d, for a total of 45.4–181.7 L water applied in each 1-m^2 plot. Two of the watering treatments triggered significant flushing of annual grasses: watering for a total of 16 d once per day, and 4 d twice per day. Although this conferred a short-term reduction in annual grass emergence at the start of the subsequent rainy season, it did not reduce total annual cover at peak flowering in the growing season, or provide a longer term advantage to native perennial grasses. It is possible that there are sufficient seeds in the seed bank that this at least partly compensated for the seed bank reduction and did not result in a reduction in final cover, or that lower densities of seedlings are sufficient to achieve "total" cover. Perennial grass cover increased in response to all watering treatments, but this did not result in significantly increased cover the following year. These results suggest that even watering treatments that produce large flushes of exotic annual grasses are insufficient to reduce exotic cover longer term. It should be explored whether more water, applied more frequently, could be effective in reducing the exotic grass seed bank enough to confer a long-term reduction in exotic cover and a benefit to native perennial grasses.

Key words: annual grass; California; exotic; flush; Mediterranean; priority effects; restoration; seasonal priority advantage; weeds.

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Introduction

Over 9.2 million hectares of California's grasslands have been largely replaced by exotic annuals (Seabloom et al. 2003), mainly annual Mediterranean grasses and forbs (Mooney and Drake 1986), which present a significant challenge in California (Stromberg et al. 2007). Restoration sites in particular are highly susceptible to invasion by these exotic annuals that can delay, reduce, or prevent success of planted native perennial grasses. Even "successful" recovery in these systems may take up to 20 yr or more after seeding with native perennial grasses, and may still fall short of native cover in undisturbed systems by more than 50%, making them susceptible to ongoing invasion (Munson and Lauenroth 2012). Early-germinating and fast-growing exotic annual grasses (operationally defined, and hereafter referred to, as "exotics," as opposed to "weeds" which could include *any* undesirable plant species) may rapidly deplete available resources—particularly water—each season before perennial grasses become active (Lowe et al. 2003). Therefore, efforts to restore native plants would benefit from a shift in the competitive balance in favor of desired plants, both before and after planting.

The ability of exotics to take early advantage of water and resources, known as a "seasonal priority advantage" or "seasonal priority effects," may reduce native plant success (Reynolds et al. 2001, Wainwright et al. 2012). Manipulation of these seasonal priority effects is a common practice among land managers wishing to reduce competition from exotics in favor or more desirable native species. Farmers and restorationists commonly apply water at large scales to induce artificial flushing of weeds, followed by lethal postflushing interventions, such as tillage and herbicide application. Additional methods for altering the seasonal priority advantage of exotics include altering the timing of planting and order in which species are introduced (Palmer et al. 1997, Vaughn and Young 2015); planting in patches to reduce competition between species with different phenology (Porensky et al. 2011); weed control, which reduces competitive pressure from undesirable plants for a short-period, giving desirable species a competitive advantage early on (Funk et al. 2008, Wainwright et al. 2012); and manipulations of water, nutrient availability, and biotic interactions with other trophic levels (Funk et al. 2008, 2015). While there are many options for promoting success of desirable plants in annual croplands and initial restoration settings—where managers start with a relatively "blank slate"—options are limited in perennial cropland or postrestoration settings.

In California's Mediterranean climate, additional summer water resources may create early circumstances favorable to native grasses, and reduce competition from exotic annual grasses in the later growing season, by allowing for native growth during the usually dormant season and increasing storage of carbohydrates, inducing an increased competitive edge over exotics in the subsequent growing season (Clary et al. 2004). In a greenhouse study simulating climate regimes of eastern Spain, Clary et al. (2004) found that drought-stressed Mediterranean perennial grasses recovered faster than a Mediterranean shrub, suggesting that the perennial grasses were able to opportunistically make better use of rare summer rainfall, contributing to its competitive success over time. Furthermore, surveys of annual and perennial grass cover in Spain and California revealed a positive correlation between perennial grass cover and warm season rainfall (Clary 2007), or proximity to the cool, moist coast (Clary 2012).

In addition to conferring an advantage to perennials by supplying water during California's long, dry summers, summer watering may also negatively impact exotics, causing them to "flush," thereby reducing their seed bank and decreasing competitive pressure on native perennial grasses in the subsequent growing season. Indeed, Wainwright et al. (2012) found summer watering to be an effective short-term strategy for reducing exotic cover in invaded southern California coastal sage scrub in San Diego County, and increasing native perennial shrub cover longer term, but exotic cover was not monitored after January (midway through the first growing season). Funk et al. (2015) showed high exotic emergence in a greenhouse watering study, but daily watering in a field setting failed to have significant effects on germination of exotics. Therefore, it is still unclear under what conditions late summer watering may stimulate germination of exotic seedlings. Subsequent cessation of watering prior to ambient rains may result in death of flushed exotic seedlings prior to setting seed, depleting the seed bank, and theoretically reducing competition with native perennial grasses in the fall.

In this study we tested whether summer watering in a restored grassland could: (1) cause substantial exotic emergence in the summer; (2) reduce exotic cover at the onset of ambient rains, and in the following growing season; and (3) increase native perennial grass cover 1 yr later.

Methods

Study site

This experiment was conducted at the U.C. Davis Experimental Ecosystem (38°31′44″ N, 121°48′38″ W) in Davis, California, USA. Davis is located in the Central Valley and has a Mediterranean climate with long, hot, dry summers and wet, cool winters. Mean annual precipitation is 44 cm, falling mostly between October and April. Average summer (dry season) maximum temperature is 32°C, and average winter (wet season) minimum temperature is 7°C. Germinating rains generally begin in the late fall, usually in October or November (Menne et al. 2015). Most exotic annual grasses present on-site germinate rapidly following ambient fall rains, while native perennial grasses tend to germinate later by several days to weeks (reviewed by Deering and Young 2006, D'Antonio et al. 2007). Soils are classified as Yolo silt loams (Natural Resources Conservation Service 2015).

A 0.5-ha grassland restoration was implemented in the fall of 2010 by drill seeding a mix of native grass species. The site was mowed to 15 cm 1 week prior to the beginning of the watering experiment in August 2012. Dominant annual grass species include *Bromus diandrus* Roth and *Hordeum murinum* L. Less abundant non-native forbs include *Kickxia elatine* (L.) Dumort., *Erodium cicutarium* (L.) Aiton and *Brassica nigra* (L.) W. D. J. Koch. Restored native grass species include *Elymus triticoides* Buckley, *Elymus glaucus* Buckley, and *Stipa pulchra* Hitch. The few exotic forbs present were hand-pulled each week from August to November. There were few native forb species present, and only *Eschscholzia californica* Cham. was present on-site at any notable, although still minimal, cover (<1%).

Experimental treatments

We established 36 1-m^2 plots separated by a 1-m buffer, with treatments replicated once within each of six blocks. We blocked the experiment to reduce interference due to variability and confounding factors resulting from potential differences in soil water and nutrient profiles across the experimental site. Six treatments (five watering, one control) were randomly assigned within each block. Water was applied from a gravity-fed tank through a hose and water wand, and amount of water applied at each watering event was monitored by flowmeter and applied at a rate of 3.75 L/min to prevent runoff, for a total of approximately 10 L in a 1-m^2 plot, or 1.1 cm per watering event. The amount of water applied at each watering event was the same across all plots, but the total amount of water varied depending on the treatment (Table 1). Watering treatments were applied for four consecutive days in each of 4 weeks for 1–4 weeks, for a total of 4–16 watering days and 1–2 watering events per day between 25 August 2012 and 21 September 2012.

Monitoring

We monitored the number of exotics (count) and native perennial grass aerial cover in the interior 0.5 m^2 of each 1-m^2 plot to reduce edge effects. We began monitoring with a prewatering baseline (24–25 August 2012), and continued to monitor approximately weekly thereafter through 10 November 2012. There were no live annual grasses at the time of the initial baseline survey; mean cover and standard deviation for perennial native grasses was 1.7% ± 1.6% across all treatment plots. Because the site was mowed prior to initial monitoring and treatment, we recorded individual species data in the growing season; prior to this counts and cover were classified as either native perennial grass or exotic (non-native annual) grass. There were no significant differences across plots at the baseline for both number of annual grass seedlings and percent cover of native perennial grass. Total and relative exotic cover was recorded at peak flowering in the following

Table 1. Experimental summer watering treatments.

Treatment code	Treatment	Week of watering (2012)	Total days of watering	Frequency (times per day)	Total H_2O applied per plot (cm/L)
Control	Control	n/a	0	0	0.0/0.0
1	Weeks 1–2	25 August–31 August	8	1	8.8/90.9
2	Week 1	25 August–31 August	4	1	4.4/45.4
3	Week 4	15 September–21 September	4	1	4.4/45.4
4	Week 4	15 September–21 September	4	2	8.8/90.9
5	Weeks 1–4	25 August–21 September	16	1	17.6/181.7

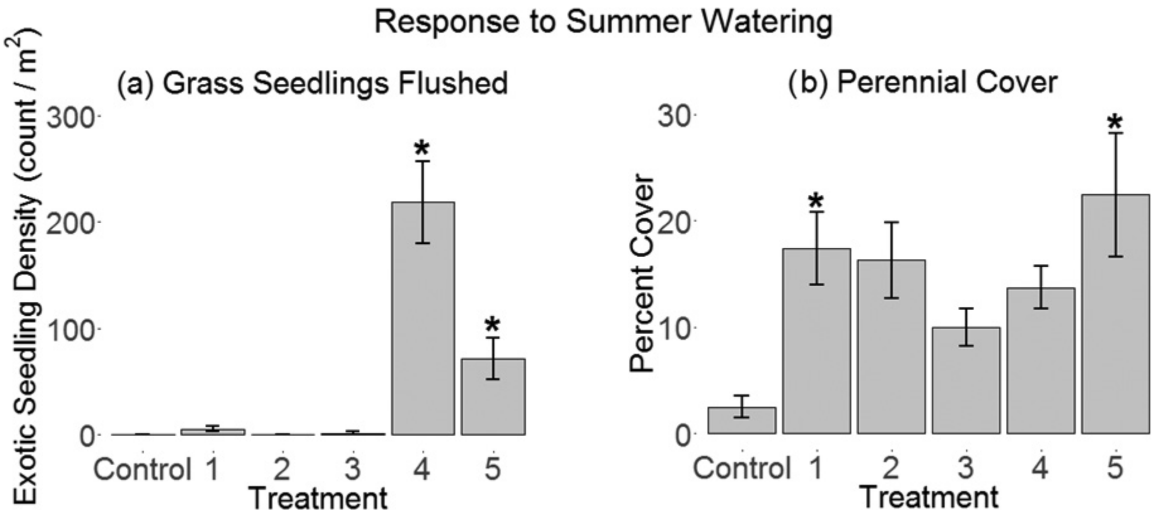

Fig. 1. Annual and perennial grass responses per 1-m^2 plot (surveyed areas restricted to interior 0.5 m^2 of each plot and results extrapolated to 1 m^2) to summer watering treatments applied between 25 August 2012 and 21 September 2012. $N = 36$; error bars are standard errors of the mean. Stars indicate Treatments that were significantly different from the Control at $\alpha = 0.05$ based on highly conservative Friedman post hoc analysis. (a) Peak exotic annual grass seedlings emerged between 1 September 2012 and 29 September 2012. One outlier in treatment 4 with 2666 seedlings was removed for easier visual comparison of average responses across all treatments. (b) Peak native perennial grass aerial cover between 1 September 2012 and 29 September 2012. Treatments: Control = no water. 1 = Weeks 1–2 (25 August 2012 – 7 September 2012), 4 d/week, once/day. 2 = Week 1 (25 August 2012 – 31 August 2012), 4 d/week, once/day. 3 = Week 4 (15 September 2012 – 21 September 2012), 4 d/week, once/day. 4 = Week 4 (15 September 2012 – 21 September 2012), 4 d/week, twice/day. 5 = Weeks 1–4 (25 August 2012 – 21 September 2012), 4 d/week, once/day.

growing season (April 2013), and native perennial grass cover was monitored in August 2013, after annual mowing.

Statistical analyses

We analyzed our randomized complete block design in R (R Core Team 2012). Due to nonnormality of data, a non-parametric Friedman chi-squared test from the "coin" package in R (Hothorn et al. 2015) was applied, which allowed for blocking. When the model was significant at $\alpha = 0.05$, the function friedman.test.with.post.hoc() was used to make all pairwise comparisons, although we were primarily interested in differences between the Treatment and Control plots; this is a highly conservative post hoc test (Galili 2010).

We compared the effects of all watering treatments at four time points: (1) Response to Summer Watering (peak number of exotic seedlings and percent native perennial grass cover in response to watering treatments were recorded for each plot in the first 5 weeks following application of watering treatments, prior to exotic death by desiccation); (2) Natural Rainfall Response (number of exotic seedlings and percent native perennial grass cover in response to subsequent natural rainfall November 2012); (3) Exotic Cover at Peak Flowering (percent cover April 2013); and (4) Perennial Cover in Summer (percent native perennial grass cover in August 2013).

Results

Response to watering treatments

Only the 4-d/twice daily (Treatment 4) and 16-d/once daily (Treatment 5) treatments experienced a significant exotic flushing response to watering (Fig. 1a; Control-Treatment 4: $P = 0.002$; Control-Treatment 5: $P = 0.007$; see means and standard errors for all treatments in Appendix

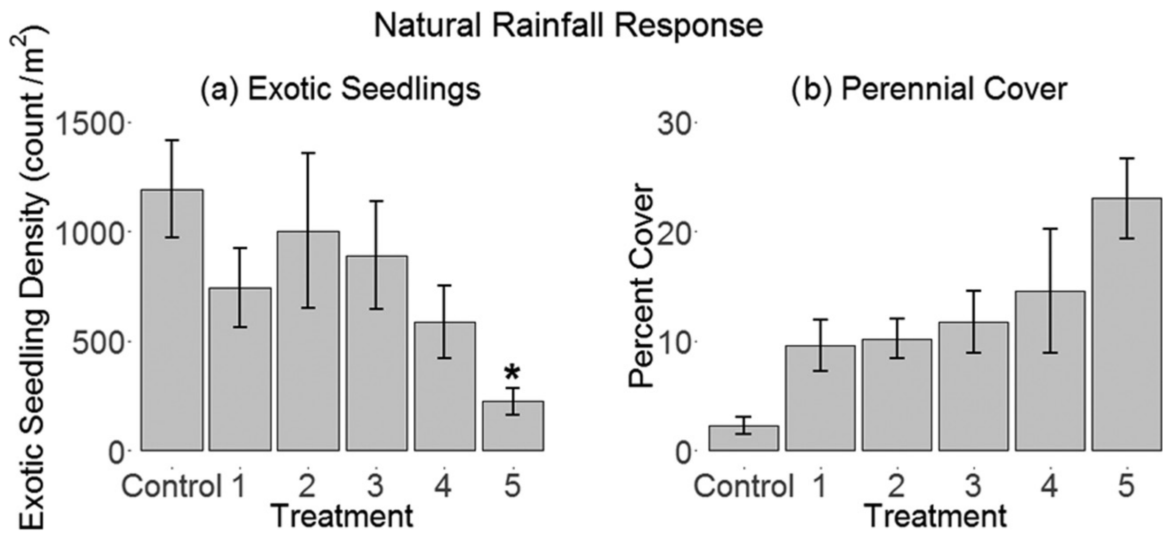

Fig. 2. Annual and perennial grass responses per 1-m^2 plot (surveyed areas restricted to interior 0.5 m^2 of each plot and results extrapolated to 1 m^2) to ambient rainfall beginning 22 October 2012, and monitored 10 November 2012. Previous summer watering treatments were applied between 25 August 2012 and 1 September 2012. $N = 36$; error bars are standard errors of the mean. Stars indicate treatments that were significantly different from the control at $\alpha = 0.05$ based on highly conservative Friedman post hoc analysis. (a) Exotic annual grass seedlings emerged. (b) Native perennial grass aerial cover. See Fig. 1 caption for treatments.

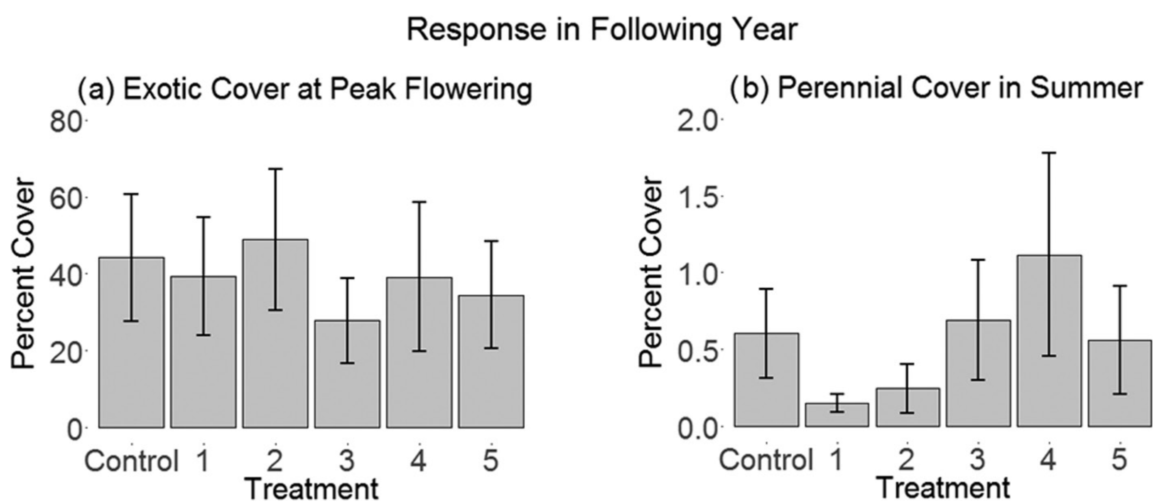

Fig. 3. Annual and perennial grass responses per 1 m^2 plot (surveyed areas restricted to interior 0.5 m^2 of each plot and results extrapolated to 1 m^2) in the year following summer watering treatments. Previous summer watering treatments were applied between 25 August 2012 and 1 September 2012. $N = 36$; error bars are standard errors of the mean. No treatments were significantly different from the Control at $\alpha = 0.05$ based on highly conservative Friedman post hoc analysis. (a) Exotic annual grass cover on 13 April 2013, at peak flowering of *Bromus diandrus* Roth and *Hordeum murinum* L. (b) Native perennial grass aerial cover on 8 August 2013, following mowing in May 2013 (note difference in scale from Figs. 1a, 2a). See Fig. 1 caption for treatments.

S1: Table S1), with mean seedling counts of 626 and 71 seedlings/m^2, respectively (no other treatment averaged more than 6 seedlings/m^2). After artificial watering ceased, all exotic seedlings died from desiccation prior to the onset of ambient seasonal rainfall. Native perennial grasses responded positively to all watering treatments, but this was significant only in the 8-d/once daily (Treatment 1) and 16-d/once daily (Treatment 5) treatments (Fig. 1b; Control-Treatment 1: $P < 0.003$; Control-Treatment 5: $P < 0.02$).

Natural rainfall response

When seasonal rains arrived in the fall (October–November), the two treatments with the greatest flushing response of exotic seedlings (Treatments 4 and 5) also had the lowest exotic seedling emergence, but only Treatment 5 had significantly lower exotic emergence than Control plots (an 80% reduction, Fig. 2a; $P < 0.005$). Native perennial grass cover in November was also higher by 22% in Treatment 5 plots (Fig 2b; $P < 0.003$) than in Control plots.

Response in year following treatment

By April 2013, when peak flowering of exotic grasses occurred, the treatments no longer differed significantly in exotic cover (Fig. 3a; $P = 0.74$) from Control plots. Despite the initially positive responses in native perennial grass cover to summer watering (Figs. 1b, 2b), and initial reductions in exotic seedlings to two watering treatments (Fig. 1a), there were no significant differences in native grass cover across treatments by the following summer, August 2013 (Fig. 3b; $P = 0.76$).

Discussion

We sought to determine whether watering treatments in the summer would (1) cause substantial germination and emergence of exotics in a hot, dry summer; (2) reduce exotic cover at the onset of ambient rains, and longer term in the following growing season; and (3) increase native perennial grass cover up to 1 yr later. If flushing depletes the exotic seed bank and/or stimulates early season perennial growth, it could increase relative success of native perennials over time.

Significant flushing (emergence) of exotics only occurred under the most intensive watering treatments (Treatments 4 and 5) with an average flush of 626 and 71 seedlings per 1-m^2 plot, respectively. Funk et al. (2015) also found that watering in the field once per day in the summer did not have a significant effect on annual cover, perhaps because the soil dried too quickly. They did report substantial germination in a concurrent greenhouse watering study, but this entailed covering of the soil to conserve soil moisture and stimulate germination. Wainwright et al. (2012) also observed only a few emerging annual grass seedlings per 2-m^2 plot in response to both August and September summer watering in a coastal sage invaded by *B. diandrus* and *Avena barbata* Link after applying 1–3 cm of water in each plot over a 1- to 3-d period. Our results suggest that substantial amounts of water, and most effectively at twice per day, are required to create a flush of exotic annuals under hot, dry field conditions, as opposed to similar amounts of rain in the cooler, moister conditions of the late fall (or in a greenhouse) (Funk et al. 2015).

The fact that the 4-d/twice-daily watering treatment (Treatment 4) was carried out only in September is unlikely to be a confounding factor. The 4-d/once-daily watering treatment initiated in September (Treatment 3) had no appreciable germination, which it shared with the 4-d/once-daily watering treatment in August (Treatment 2). Treatment 4, which occurred concurrently with Treatment 3, did, however, produce a significant flushing response. The twice-daily watering—and not the calendar date—was thus responsible for the significant seedling flush. Moreover, daily high temperature conditions across Treatments 2–4 differed by <1°C on average. To our knowledge, this is the first experiment that tested inducing summer germination of exotics by watering multiple times per day. Keeping the soil moist throughout the day was apparently important to producing a significant flushing response.

The only two treatments that stimulated a significant flushing response due to summer watering (Treatments 4 and 5) also resulted in 50% and 81% reductions, respectively, in subsequent natural seasonal germination as compared to Control plots. The reduction in natural germination in Treatment 5 at the start of ambient rainfall (mean reduction of 970 seedlings/m^2) was far greater than the documented summer flush (mean emergence of 71 seedlings/m^2), suggesting that there were far more summer germinants than we observed, perhaps because many germinating seeds did not emerge aboveground before dying. Germinating seeds that die prior to emergence—while rarely documented during field monitoring—may play an important, but not directly observed, role in reducing the exotic seed bank (James et al. 2011).

For the amount of water applied and time invested, the 4-d/twice-daily watering treatment (Treatment 4) was the most effective at flushing exotics, and the most feasible. However, while the most promising treatments (Treatments 4 and 5) did show substantial flushing in response to summer watering, resulting in pre-reproductive death after cessation of watering, none of the treatments conferred a longer term (through the following growing season, and 1 yr later) reduction in exotic cover, or an increase in native perennial grass cover. In fact, all watering treatments produced some observable exotic flushing response, and a flush of growth from native perennial grasses, but by the end of the growing season neither this nor the initial significant reduction in exotic cover in Treatment 5 resulted in greater cover by natives than unwatered Controls.

There are several potential reasons that even the "successful" watering treatments did not lead to a longer term reduction in exotic cover or an increase in perennial cover. The number of seeds produced by exotics may be so high that one artificial flushing event was not sufficient to reduce the seed bank enough to reduce exotic cover (DiVittorio et al. 2007). However, the initial lower exotic emergence during the fall rains in treatments with strong summer flushing does support the possibility that the seed bank was at least reduced.

Under natural rainfall conditions, a large number of seedlings will emerge at the onset of ambient rains, but many of them die by "self-thinning." These self-thinned seedlings then provide nitrogen to surviving or later germinating seedlings (Eviner and Firestone 2007). It is possible that the large number of seedlings that died after the artificial summer watering produced such a fertilization effect that this allowed more individual plants to survive than usual, or that surviving individuals grew larger, than would have occurred under unaltered conditions. It could also be that the level of plant available nutrients did not change, and that a reduction in the seed bank did result in a lower number of exotics, but that this was still more than enough to saturate the carrying capacity of adult annuals that survive self-thinning. Although the exotic seed bank was reduced by flushing, even these lower densities of seedlings may still have been sufficient to achieve high ("total") exotic cover.

Although perennial cover did increase briefly in Treatments 1 and 5, this significant difference disappeared by the following year (monitored the following August, 1 yr later). Compensation by exotics (Seabloom et al. 2003, Eviner and Firestone 2007) may have ultimately led to no significant difference between watered and unwatered (Control) treatments, despite initial differences in response to watering treatments, and later on at the start of the growing season (November, 3 months following watering treatments).

Management implications

Management of exotic annual grasses in restored grasslands is challenging because grass-specific herbicides usually cannot be applied, and even when they can, timing and dosage of application is critical to minimize negative impacts on perennial grasses that may not be dormant at the time of the fall exotic flush (Laude 1953, Volaire and Norton 2006). Reduction of competitive pressure via flushing of exotics is commonly practiced in croplands and prerestoration settings (Stromberg and Kephart 1996, Fitzpatrick 2004), when it can be accompanied by lethal postflushing interventions other than desiccation, like tillage or herbicides. It was our hope that flushing and desiccation alone might be an effective way of reducing weed challenge without harming (and perhaps directly helping) native perennial grasses.

This study revealed that watering at the levels used in this experiment did not result in a significant long-term reduction in exotic cover, or a significant increase in native perennial grass cover (via either direct or indirect effects). However, the twice-daily watering treatment (Treatment 4) produced the most promising results, at least for initial exotic flushing. Watering once per day was only effective for flushing exotics if continued over a 4-week period (Treatment 5), which is a long time commitment for already time-pressed managers (Funk et al. 2015). As in Funk et al. (2015), the greatest cost to this method is the time required to apply watering treatments, although greater areas could be covered by industrial sprinklers with a lower daily time commitment (as is practiced in many local, large agricultural production systems for much longer durations). Applications of this method at small restoration sites may be more feasible, or it could be applied on larger restorations in a patchwork to introduce spatial heterogeneity, which could also prove useful for providing native floral refuges. Additional testing of the long-term implications of increased daily frequency of watering should be investigated.

Keeping the soil moist between watering is apparently critical to inducing a strong flushing response in a reasonable period of time (in this case, watering twice per day for only 4 d produced a larger peak flushing response than watering once per day for a total of 16 d). Our results would likely be different if water was applied in cooler, cloudier fall or winter seasons, as suggested by Gulmon (1992) and Funk et al. (2015). However, the risk of germinants flowering may be increased under this circumstance if seedling death is not ensured by tillage, herbicide, or other methods (Wainwright et al. 2012), particularly if germinating rains begin earlier than usual. Grazing combined with native grass seeding may also be an effective method for reducing invasive cover, and potentially increasing native species richness, although native cover may also be reduced (Funk et al. 2015). Finally, applications of this method over a period of several consecutive years may produce longer lasting results, although this has not been tested. If extended to an increased number of waterings per day or increased amount of water—an as yet untested method—this postrestoration watering strategy, may yet prove to be effective long-term in reducing exotic grass cover, and/or increasing native perennial grass cover.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1309/supinfo