Restoration Ecology
THE JOURNAL OF THE SOCIETY FOR ECOLOGICAL RESTORATION

TECHNICAL ARTICLE

Repeated mowing to restore remnant native grasslands invaded by nonnative annual grasses: upsides and downsides above and below ground

Justin M. Valliere[1,2], Susan Balch[3], Carole Bell[4], Carlos Contreras[5], Bridget E. Hilbig[6]

California grasslands have been severely impacted by the invasion of nonnative annual grasses, which often limit restoration of this important ecosystem. In this study, we explored the use of mowing as a restoration tool for native perennial grasslands at the Santa Rosa Plateau Ecological Reserve in southern California. We sought to evaluate if, over time, mowing would reduce nonnative annual grass cover and benefit native species, especially the native bunchgrass *Stipa pulchra*. We hypothesized that repeated mowing, carefully timed to target nonnative annual grasses prior to seed maturation, would reduce nonnative seed inputs into the soil and eventually lead to diminished abundance of these species. We monitored vegetation in mowed and unmowed plots for 4 years, and conducted a seed bank study after 5 years to better understand the cumulative effects of mowing on native and nonnative seed inputs. Consistent with our hypotheses, we found that mowing successfully reduced nonnative annual grass cover and benefitted some native species, including *S. pulchra*. However, we also found that nonnative forb species showed progressive increases in mowed plots over time. We observed similar patterns of species composition in the soil seed bank. Together, these results suggest that mowing can be used to control nonnative annual grasses and increase the abundance of native bunchgrasses, but that this method may also have the unintended consequence of increasing nonnative forb species.

Key words: California perennial grasslands, ecological management, grassland restoration, invasive species, mowing, phenological niche, *Stipa pulchra*

Implications for Practice

- Mowing may be an effective tool for reducing the seed bank of nonnative species if two conditions are met: it is carefully timed to be maximally destructive to nonnatives *and* it is not harmful to native species.
- This method may need to be paired with additional weed control measures if there is more than one species of concern. This is especially true if there are nonnative species present that are not impacted (or benefitted) by mowing.
- The success of this approach also depends on the presence of remnant native species, either above ground or in the soil seed bank. In some cases, native seed addition or outplanting may be necessary to facilitate the recovery of target species.

Introduction

Native perennial grasslands in California represent one of the most biodiverse yet most endangered habitats in the United States (Murphy & Ehrlich 1989; Skinner & Pavlik 1994). These grasslands, consisting of perennial bunchgrasses and annual and perennial forbs, once covered vast stretches of California's coasts, foothills, and valleys (Schiffman 2007). However, California grasslands changed dramatically with the arrival of Europeans to the North American continent and subsequent cattle grazing, agriculture, land development, and nonnative plant invasion (Murphy & Ehrlich 1989). Today only a fraction of native grasslands remain, and even the least-disturbed remnants are heavily invaded by nonnative plant species, with annual grasses from the Mediterranean being the most problematic (Baker 1989).

California's grasslands have been so severely impacted since European settlement that there is some uncertainty regarding

Author contributions: JV, BH, CB, SB designed field experiments; JV, BH managed vegetation monitoring; CB mowed experimental plots each year; JV, CC performed the seed bank study; JV, BH analyzed the data and wrote the manuscript; all authors provided editorial review.

[1]La Kretz Center for California Conservation Science, University of California Los Angeles, Los Angeles, CA 90095, U.S.A.
[2]Address correspondence to J. M. Valliere, email valliere@ucla.edu
[3]Shivela Middle School, Murrieta Valley Unified School District, Murrieta, CA 92562, U.S.A.
[4]The Nature Conservancy, Santa Rosa Plateau Ecological Reserve, Murrieta, CA 92562, U.S.A.
[5]Department of Ecology and Evolutionary Biology, University of California Los Angeles, Los Angeles, CA 90095, U.S.A.
[6]Department of Botany, Weber State University, Ogden, Utah 84408, U.S.A.

doi: 10.1111/rec.12873
Supporting information at:
http://onlinelibrary.wiley.com/doi/10.1111/rec.12873/suppinfo

their original composition and the historical dominance of native bunchgrasses (Schiffman 2007; Minnich 2008). The reality today, however, is that even the best-preserved grasslands have a high density of nonnative species, and in many places what little native vegetation remains is often perennial bunchgrasses (Bartolome & Gemmill 1981; Hamilton 1997) such as *Stipa pulchra* (purple needlegrass).

Due to the widespread destruction and degradation of these grasslands, there has been much interest in their management and restoration (Stromberg & Griffin 1996; Stromberg et al. 2007). Perhaps the greatest limitation to native grassland restoration is the presence of nonnative annual grasses such as *Avena* and *Bromus* species. These species outcompete native bunchgrasses (Nelson & Allen 1993; Corbin & D'Antonio 2010) and severely limit the reestablishment of native seedlings (Bartolome & Gemmill 1981; Fossum 1990). Therefore, control of these invaders, through grazing, burning, herbicide, tilling, or mowing, is often a priority in grassland restoration (Ditomaso et al. 2007). Traditional grassland restoration techniques such as seeding or outplanting of nursery-grown individuals are necessary where native species have been extirpated. However, if some native species persist, it is possible that targeted weed management efforts alone could aid in the restoration of remnant grassland habitat.

Mowing may be a useful restoration method for controlling nonnative annual grasses in remnant grasslands if carefully timed to target these species, but few studies have tested this (Stromberg et al. 2007). Working in grasslands of northern California, Maron and Jefferies (2001) showed that mowing reduced annual grasses and benefitted native species. Similar results were also reported in semi-arid grasslands outside of California invaded by barb goatgrass, *Aegilops triuncialis* (Aigner & Woerly 2011) and cheatgrass, *Bromus tectorum* (Prevéy et al. 2014. Other studies have yielded mixed results. For example, Hayes and Holl (2003) found that at some grassland sites along the central California coast, vegetation clipping merely shifted the community from nonnative grasses to nonnative forbs. Kimball and Schiffman (2003) reported similar increases in nonnatives coupled with negative effects on natives. Frequent mowing could also act as a disturbance, perpetuating the dominance of nonnative annual grasses (Seabloom et al. 2003*a*). Thus, the value of this approach may be very site-specific and it is not well understood. Furthermore, previous work has focused exclusively on aboveground vegetation, and none of these aforementioned studies examined the effects of this treatment on the composition of soil seed banks.

In this study, we explored the use of repeated mowing as a restoration tool to manage remnant perennial grasslands of southern California. Our goal was to assess the impact of mowing on the relative cover of native and nonnative species, especially the native bunchgrass, *S. pulchra*, and nonnative annual grasses. Given that the seeds of many annual grasses are relatively short-lived in the soil (Lewis 1973; Marañón & Bartolome 1989), we hypothesized that repeated mowing would reduce their dominance if timed to prevent the input of mature seeds to the seed bank (Stromberg et al. 2007). We also hypothesized that by controlling nonnative annual grasses, mowing would result in increased cover of native species over time. If successful, this approach could provide practitioners with a useful tool for managing remnant native habitat that may be less resource-intensive than traditional methods of restoration and weed management.

Methods

Study Site

We conducted field research at the Santa Rosa Plateau Ecological Reserve (Fig. 1A; Tables S1) located near Murrieta, California (33°30′46″N, 117°16′37″W), which is home to some of the best-preserved perennial grasslands in the state. The reserve consists of large expanses of grassland intermixed with oak woodlands, and experiences a Mediterranean-type climate with hot, dry summers and cool, wet winters. Mean annual precipitation is 550 mm, most of which falls from December to April. Elevation at the reserve is about 610 m. The study site was located in a grassland plant community typical of the reserve, consisting of native bunchgrasses and forbs, nonnative forbs, and a high density of nonnative annual grasses.

Experimental Design

The study site was approximately 70 × 50 m, which was divided into four subplots (Fig. 1B). Two subplots were assigned as unmowed controls, and the other two were mowed each year in the spring using a tractor with the mowing blade at a height of approximately 15 cm, beginning in 2012. Mowing was completed each year prior to seed set of the dominant nonnative grasses (*A. fatua* and *Bromus* species) and before flowering of native bunchgrasses, with the goal of reducing the number of viable seeds entering the soil seed bank. The timing of seed development in target nonnative grasses was determined by regular field surveys by C. Bell, the reserve manager. Vegetation cover was measured each year in the spring before mowing along six permanent transects that run parallel across the plots. Each transect is 40 m long, spanning both mowed and control subplots (20 m for each treatment). Vegetation cover and density were sampled in 1 m^2 quadrats placed every 5 m along each transect, for a total of 30 quadrats per treatment.

Citizen Scientists

From 2014 to 2016, field data was collected by eighth grade students from Shivela Middle School in Murrieta, California, under the supervision of S.B., B.H., and J.V. as part of the Santa Rosa Plateau Foundation's Habitat Studies and Restoration Program. Students visited the site multiple times per year and received training on grassland ecology, plant identification, and vegetation sampling prior to collecting data in the spring. Data for the 2016–2017 growing season was collected by J.V.

Seed Bank Study

We conducted a seedling emergence study using soils collected in October 2017 from the study site to understand the effects of

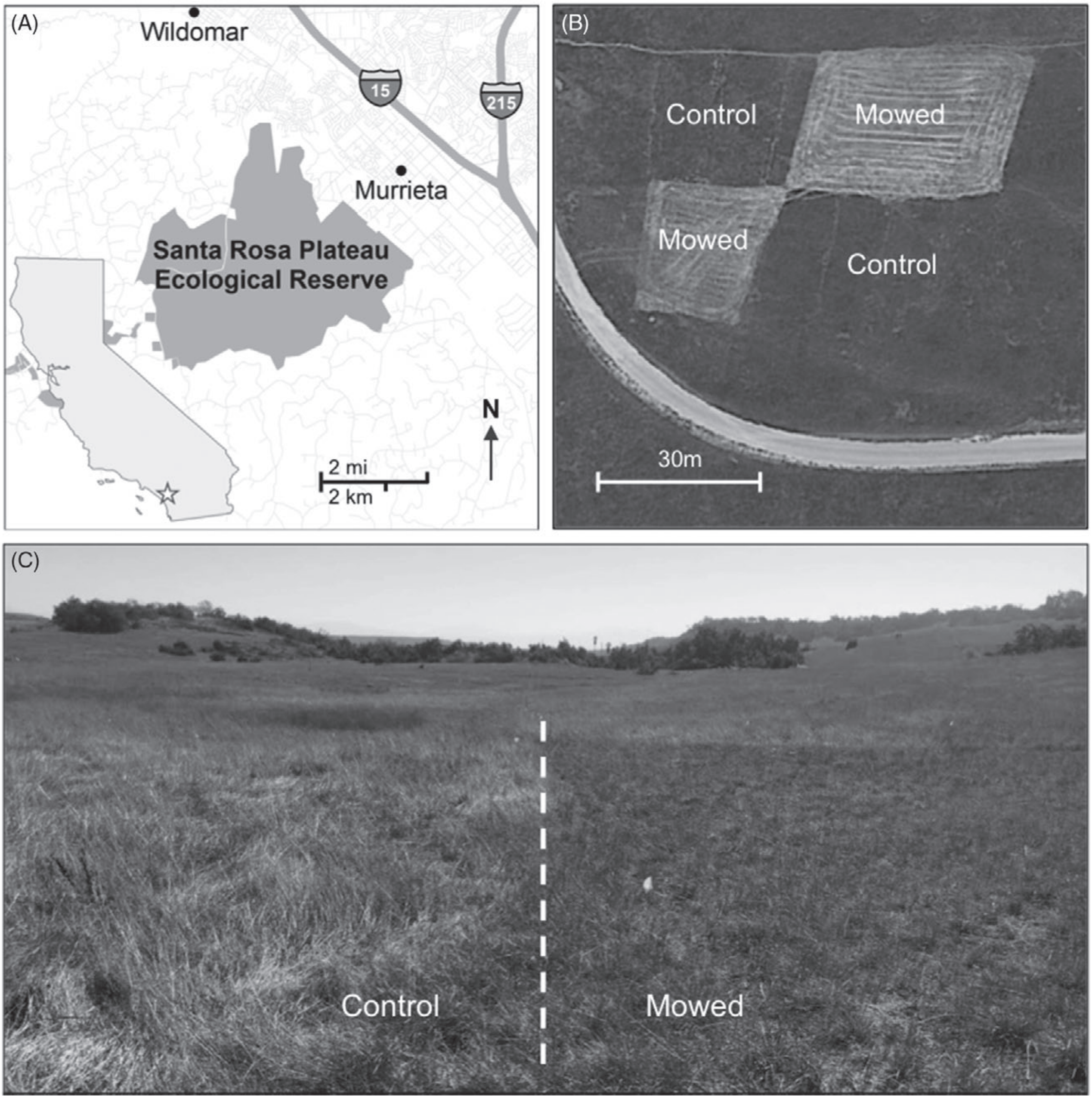

Figure 1. Location of the Santa Rosa Plateau Ecological Reserve in southern California (A), aerial view of the study site (B), and a photograph from fall 2015 showing mowed and unmowed portions of the plot (C). Note reductions in annual grass litter and visible crowns of perennial bunchgrasses in the mowed subplot.

mowing on soil seed bank composition. Within each vegetation sampling quadrat, we took two soil cores (including litter) 10 cm in diameter and 5 cm in depth with a distance of approximately 50 cm between samples. The two cores from each quadrat were pooled, resulting in a total of 30 soil samples for each treatment. We conducted the study from November 2017 to February 2018 on outdoor benches at the University of California, Los Angeles. We placed soil samples on top of the sterile potting soil in 1 gal pots and watered the pots 1–2 times per week as needed. As seedlings germinated, we identified each species, and these were counted and removed to prevent re-counting in future surveys. Unknown plants were allowed to grow until identifying characteristics emerged. After 1 month, germination ceased, so we stirred soils in each pot and resumed watering and collecting data. This was repeated again 1 month later, and soils were also treated with 250 mL/pot of a 10% solution of liquid smoke (Colgin Inc., Dallas, Texas, U.S.A.). Smoke water treatments are commonly used in seed bank studies to elicit germination, especially, in soils from fire-prone ecosystems. We ended the experiment after tracking full 3 months of germination.

Statistical Analysis

Percent cover data for each species and/or native and nonnative functional group was analyzed with a linear mixed-effects model in which treatment (mowing or control), year, winter precipitation, and mean January low temperature were fixed effects and transect was a random effect. Climate data were retrieved from Oregon State University's PRISM database (http://www.prism.oregonstate.edu/). We added transect as a random effect due to the fact that each transect had multiple data collection points (five 1 m^2 quadrats per treatment/transect), and transects may have varied slightly in aspect or microclimate for seed germination. The proportion of the total variation they account for was calculated and is reported as a percentage. p Values were estimated using likelihood ratio tests in which linear mixed-effects models were compared to null models without the factor of interest in them. Seed bank data were analyzed by plant species and functional group using Wilcoxon–Mann–Whitney tests. All analyses were performed in R (RStudio Version 1.1.419).

Results

Aboveground Vegetation

Overall, bare ground cover (Fig. 2A) was greater in mowed plots compared to controls ($\chi^2 = 19.7$, $df = 1$, $p < 0.0001$). There was no significant effect of year ($\chi^2 = 0.21$, $df = 1$, $p = 0.65$), winter precipitation ($\chi^2 = 1.01$, $df = 1$, $p = 0.32$), or mean January low ($\chi^2 = 0.5$, $df = 1$, $p = 0.38$) on bare ground. Transect accounted for <1% of the total variance. Litter declined with mowing ($\chi^2 = 14.7$, $df = 1$, $p = 0.0001$), but year ($\chi^2 = 3.97$, $df = 1$, $p = 0.05$) and winter precipitation ($\chi^2 = 4.00$, $df = 1$, $p = 0.04$) also had a significant effect (Fig. 2B). January temperature had no significant effect on litter cover ($\chi^2 = 3.08$, $df = 1$, $p = 0.08$), and transect accounted for 4.1% of the total variance. Percent cover of the native bunchgrass *Stipa pulchra* increased with mowing ($\chi^2 = 35.8$, $df = 1$, $p < 0.0001$; Fig. 2C), while year ($\chi^2 = 0.17$, $df = 1$, $p = 0.68$), winter precipitation ($\chi^2 = 1.24$, $df = 1$, $p = 0.27$), and mean January low ($\chi^2 = 1.46$, $df = 1$, $p = 0.24$) had no significant effect, and transect accounted for 1.5% of the total variance. Conversely, nonnative annual grass cover declined in mowed plots compared to controls from 2014–2017 ($\chi^2 = 62.78$, $df = 1$, $p < 0.0001$; Fig. 2D), and was lower in years with lower January temperatures ($\chi^2 = 5.32$, $df = 1$, $p = 0.02$). Year ($\chi^2 = 3.61$, $df = 1$, $p = 0.06$) and winter precipitation ($\chi^2 = 0.33$, $df = 1$, $p = 0.56$) had no significant effect on annual grass cover, and transect only accounted for 3.0% of the total variance. Treatment ($\chi^2 = 3.25$, $df = 1$, $p = 0.07$), year ($\chi^2 = 1.89$, $df = 1$, $p = 0.17$), winter precipitation ($\chi^2 = 3.66$, $df = 1$, $p = 0.06$), and mean January low ($\chi^2 = 1.36$, $df = 1$, $p = 0.24$) did not influence native forb cover (Fig. 2E). Percent coverage of nonnative forbs was higher in mowed than control plots in all years ($\chi^2 = 60.4$, $df = 1$, $p < 0.0001$; Fig. 2F). No other variables in mixed-effects models had a significant effect on nonnative forb cover, and transect accounted for just 3.9% of the total variation.

Soil Seed Bank Composition

After 5 years, mowing had a significant effect on species composition of the soil seed bank (Table 1), yielding similar patterns as aboveground vegetation including reduced abundance of some annual grass species, especially *Avena fatua* ($p < 0.0001$; Table 1), and increased numbers of seeds of *S. pulchra* ($p < 0.0001$; Table 1). About 25 species germinated from the seed bank, of which 11 species were native to California. Overall, native forb species responded positively to mowing, driven largely by increased numbers of seeds of *Deinandra fasiculata* ($p < 0.0001$; Table 1). Seeds of nonnative forbs including *Erodium brachycarpum* and *Hypochaeris glabra* were also present in significantly higher numbers in mowed versus control plots ($p < 0.0001$; Table 1).

Discussion

The results of this experiment reveal several important points relevant to the management of invaded perennial grasslands: (1) carefully timed mowing may be an effective method to reduce nonnative annual grasses by minimizing seed inputs to the soil seed bank; (2) native perennial bunchgrasses and some native forbs may benefit from springtime mowing; and (3) this method may also increase the abundance and cover of nonnative forbs. We also observed substantial year-to-year variability and significant effects of climate variables on some plant species. For example, native forb species were almost entirely absent in some years, and nonnative annual grass cover tended to be higher in years with warmer January temperatures. Longer-term monitoring and replication across sites will be useful in determining the broad-scale utility of this approach and the influence of environmental variability.

Mowing Reduces Nonnative Annual Grass Cover

The ability to reduce the abundance of nonnative grasses while benefitting native grasses stems from key phenological differences among these species (Wolkovich & Cleland 2011). Nonnative grasses such as *Avena fatua* are winter-active annuals that germinate rapidly with the first rains of the season, flowering and setting seed earlier in the spring. In contrast, the native perennial bunchgrass *Stipa pulchra* is typically slow to initiate growth in the cooler months of early winter, becoming more active only once warmer springtime temperatures arrive (Hull & Muller 1977). Indeed, the earlier phenology of these annual grasses—or seasonal priority advantage—is likely a major contributor to their success (Wainwright et al. 2012). However, by exploiting this lag between the growth and reproduction of these species, practitioners may be able to dramatically reduce seed production of annual grasses through springtime mowing without harming natives, as shown here. These results are consistent with previous studies in other semi-arid grasslands showing that mowing may be an effective way to control nonnative annual grasses (Maron & Jefferies 2001; Aigner & Woerly 2011; Prevéy et al. 2014).

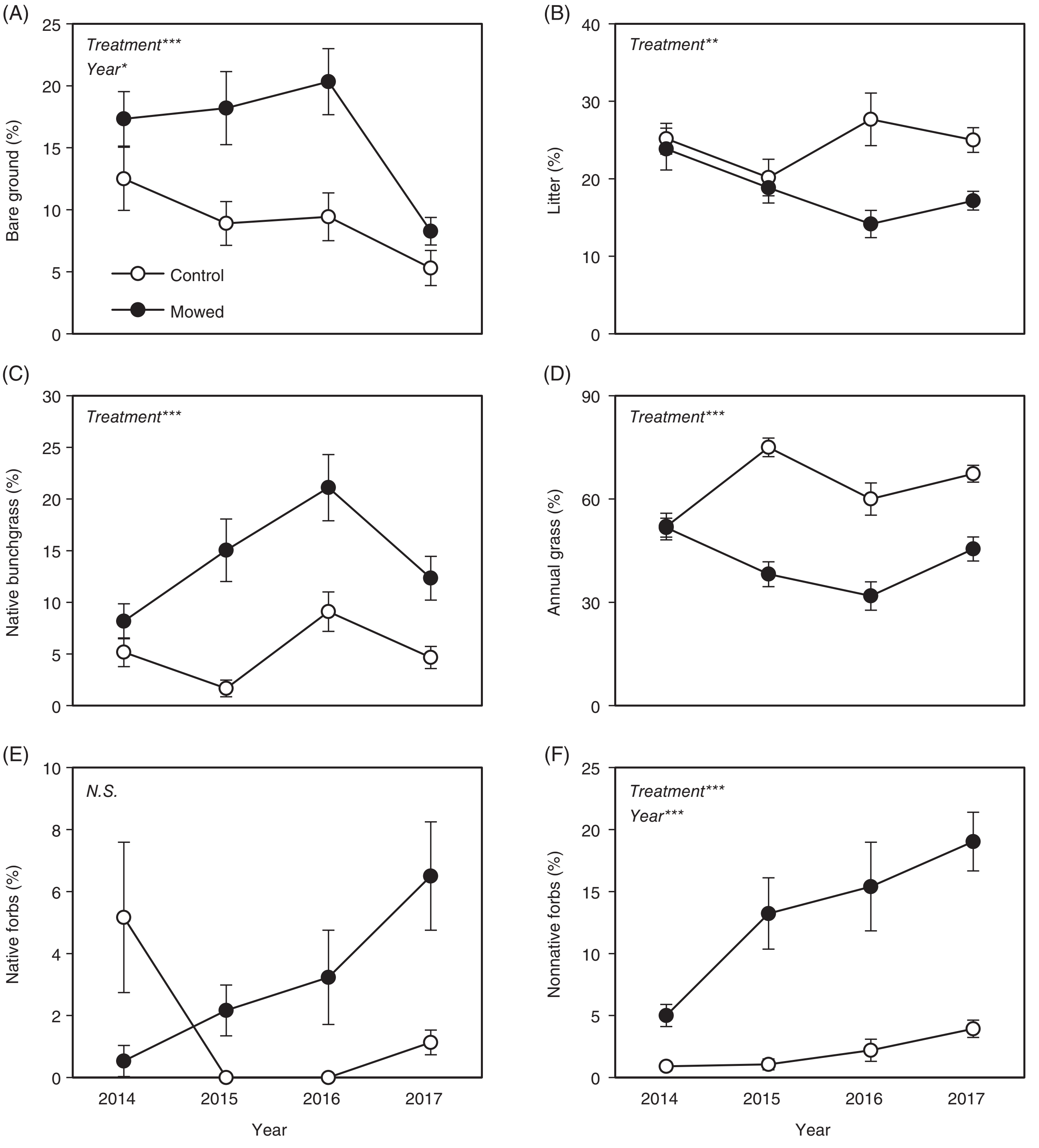

Figure 2. Percent cover of bare ground (A), litter (B), and native and nonnative plant functional groups including the native bunchgrass *Stipa pulchra* (C), nonnative annual grasses (D), native forbs (E), and nonnative forbs (F). Significant effects of treatment and year are also shown (*$p < 0.05$, **$p < 0.001$, ***$p < 0.0001$). Error bars represent ± SE.

Our study is unique in that the results of our soil seed bank study demonstrate a clear reduction in the number of seeds of annual grasses in the soil, especially *A. fatua*. This strongly suggests that reduced seed production of these species with mowing was the mechanism that contributed to lower cover of these species aboveground. The seeds of *A. fatua* and other annual grasses are not long lived in the soil seed bank and there is little carryover from year to year (Lewis 1973). Thus, it may be possible to exhaust the seed bank of these species in as little as a few years of mowing. It is important to note that

Table 1. Mean seed density of plant species and native and nonnative plant functional groups by treatment (mowed or unmowed controls) ± SE. Values represent number of seeds/m^2 based on the size of soil cores taken for soil seed bank analysis. Significant differences are shown in bold (from Wilcoxon–Mann–Whitney tests).

Plant species	*Mean seeds/m^2*				*Chi-square*	df	p
	Control		*Mowed*				
Native species							
Acmispon americanus	0	–	1	±1	0.81	1	0.3689
Ambrosia psilostachya	0	–	1	±1	0.40	1	0.5295
Calindrinia ciliata	1	±1	2	±1	1.98	1	0.1595
Corethrogyne filaginifolia	0	–	2	±1	2.98	1	0.0842
Deinandra fasiculata	**2**	**±1**	**38**	**±1**	**24.59**	**1**	**<0.0001**
Dichelostemma capitatum	1	±1	0	–	0.81	1	0.3689
Ranunculus californicus	0	–	1	±1	0.40	1	0.5295
Stipa pulchra	**7**	**±1**	**25**	**±4**	**20.74**	**1**	**<0.0001**
Nonnative species							
Avena fatua	**698**	**±57**	**42**	**±5**	**43.88**	**1**	**<0.0001**
Anagallis arvensis	1	±1	0	–	1.27	1	0.2597
Bromus diandrus	**25**	**±5**	**5**	**±2**	**17.65**	**1**	**<0.0001**
Bromus rubens	162	±31	171	±21	0.38	1	0.5394
Centaurea melitensis	1	±1	0	–	0.40	1	0.5295
Erodium brachycarpum	**6**	**±3**	**79**	**±11**	**32.63**	**1**	**<0.0001**
Erodium cicutarium	**2**	**±1**	**18**	**±8**	**5.43**	**1**	**0.0197**
Festuca perennis	2	±1	2	±1	0.05	1	0.9340
Hirschfeldia incana	3	±1	1	±1	3.42	1	0.0645
Hypochaeris glabra	**33**	**±6**	**10**	**±4**	**19.24**	**1**	**<0.0001**
Lactuca serriola	1	±1	0	–	0.40	1	0.5295
Medicago polymorpha	1	±1	0	–	0.40	1	0.5295
Sonchus oleraceous	6	±2	3	±1	1.21	1	0.2718
Plant functional groups							
Native bunchgrasses	**7**	**±2**	**25**	**±4**	**20.74**	**1**	**<0.0001**
Native forbs	**3**	**±1**	**33**	**±5**	**28.18**	**1**	**<0.0001**
Nonnative annual grasses	**887**	**±52**	**220**	**±21**	**43.68**	**1**	**<0.0001**
Nonnative forbs	**51**	**±7**	**112**	**±15**	**13.13**	**1**	**0.0003**

while the number of seeds of *A. fatua* and *Bromus diandrus* were significantly reduced in mowed plots, *Bromus rubens* was unaffected, possibly because of its shorter stature.

Positive Effects on Native Bunchgrasses

We observed positive effects of mowing on the cover of the native bunchgrass *S. pulchra*, and increased numbers of seeds of this species in the soils of mowed plots further suggest that mowing may have stimulated greater seed production of this species. This positive response is likely due to reduced competition from annual grasses (Dyer & Rice 1997; Corbin & D'Antonio 2004), especially for soil moisture (Davis & Mooney 1985). Mowing may also have had a positive effect on seed quality in this species, leading to a higher number of viable seeds in the soil. For example, Dyer (2002) found that grazing of *S. pulchra* resulted in the production of seeds with higher germination than those from untreated control plants.

Mowing Increases Nonnative Forbs

One potential drawback to this approach is the risk of trading one nonnative invader for another, such as the observed shift from nonnative annual grasses to nonnative forbs. This was primarily because of increases in *Erodium* species, including *Erodium cicutarium* and *Erodium brachycarpum*. These low-growing, rosette-forming forbs are generally shorter than the height of the mower blade used to treat plots, giving them an advantage over taller species. Furthermore, mowing likely increases colonization sites and reduces competition from annual grasses that previously held these species in check. This is similar to the results of a mowing experiment in grasslands of Colorado, where mowing shifted the community from nonnative annual grasses to forbs, including *E. cicutarium* (Prevéy et al. 2014). Experimental grazing yielded the same result in California grasslands, where *Erodium* species responded positively (Kimball & Schiffman 2003). Burning also shifted annual grasses to *Erodium* domination in a previous study at the Santa Rosa Plateau (Gillespie & Allen 2004). In some cases, these nonnative forbs may be preferable to annual grasses, especially if native species also benefit (Cox & Allen 2011), but practitioners should be wary of secondary invasion by more problematic species (Pearson et al. 2016). Pairing mowing with other weed control methods that target nonnative forbs, such as broadleaf herbicides, could facilitate greater native recovery (Ditomaso et al. 2007).

Possible Benefits of Mowing for Native Forbs

Native forbs were a relatively minor component of the vegetation at our site during the study period, and aboveground cover of these species showed no response to mowing. The density of native forb seeds was significantly higher in mowed plots compared to controls, but this was driven largely by a single species, *Deinandra fasciculata*. We did not observe increased cover of this species, but it is likely we missed the peak growth of this late-season annual during spring sampling. However, overall seeds of most observed species were not present in high numbers in the soil, suggesting seed limitation may be hampering their recovery even as annual grass density is reduced (Seabloom et al. 2003*b*). Therefore, seeding native forb species in conjunction with mowing may be a successful restoration strategy in California grasslands.

Other Benefits of Mowing

These results may be comparable to other control methods carefully timed to target annual grasses. However, mowing may not carry the same risks and complications as prescribed fire, herbicides, or livestock grazing. This method may also have other ecological benefits. For example, mowing may improve habitat suitability for native songbirds of California grasslands by increasing native plant cover, bare ground, and heterogeneity of vegetation structure (Gennet et al. 2017). Reduced dominance of annual grasses may also lower fire risk in California grasslands by minimizing the accumulation of highly flammable litter (D’Antonio & Vitousek 1992). Finally, this study also provides a successful example of how collaboration with researchers and citizen scientists can provide practitioners with valuable information on the efficacy of potential restoration techniques.

Acknowledgments

We would like to thank the Santa Rosa Plateau Foundation for supporting this work through the Habitat Studies and Restoration Program, especially Executive Director G. Greaves. S. Hanson, R. Hicks, J. Lockyer, M. Bell, and A. Swanson provided assistance in the field. Edith Allen (University of California, Riverside) provided useful advice throughout the study. Finally, we would like to thank the many students from Shivela Middle School in Murrieta for their hard work monitoring this field experiment and contributing to the success of this citizen science project. Two anonymous reviewers also provided valuable feedback on a previous draft of this paper.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. List of plant species observed at the study site and in the soil seed bank.

Coordinating Editor: Lora Perkins

Received: 17 March, 2018; First decision: 6 July, 2018; Revised: 2 August, 2018; Accepted: 2 August, 2018