


RESEARCH ARTICLE

Using consecutive prescribed fires to reduce shrub encroachment in grassland by increasing shrub mortality

Peter Hopkinson^{1,2} , Michele Hammond^{1,3}, James W. Bartolome¹, Luke Macaulay¹

Woody plant encroachment into open grasslands occurs worldwide and causes multiple ecological and management impacts. Prescribed fire could be used to conserve grassland habitat but often has limited efficacy because many woody plants resprout after fire and rapidly reestablish abundance. If fire-induced mortality could be increased, prescribed fire would be a more effective management tool. In California's central coast, shrub encroachment, especially of *Baccharis pilularis* (coyote brush), is converting coastal prairie into shrub-dominated communities, with a consequent loss of native herbaceous species and open grassland habitat. *B. pilularis* has not been successfully controlled with single prescribed fire events because the shrub resprouts and reestablishes cover within a few years. We investigated whether two consecutive annual burns would control *B. pilularis* by killing resprouting shrubs, without reducing native herbaceous species or encouraging invasive plants. As expected, resprouting did occur; however, 2 years after the second burn, *B. pilularis* cover on burned plots was only 41% of the cover on unburned plots. Mortality of *B. pilularis* more than doubled following the second burn, likely maintaining a reduction in *B. pilularis* cover for longer than a single burn would have. Three native coastal prairie perennial grasses did not appear to be adversely affected by the two burns, nor did the burns result in increased cover of invasive species. Managers wanting to restore coastal prairie following *B. pilularis* encroachment should consider two consecutive annual burns, especially if moderate fire intensity is achievable.

Key words: *Baccharis pilularis*, *Brachypodium distachyon*, native grass, resprouting, *Stipa pulchra*, woody plant encroachment

Implications for Practice

- Two consecutive annual burns controlled *Baccharis pilularis* effectively by increasing shrub mortality.
- Fire appeared to result in increased *B. pilularis* mortality and slower shrub cover recovery on steeper slopes, while wetter and flatter areas experienced lower mortality and faster recovery.
- The two consecutive burns did not appear to harm desirable native herbaceous species nor encourage invasives.
- Fire can be an effective tool for long-term maintenance of open grassland, but its use is required relatively regularly to achieve desired results.
- We recommend burning before shrubs have occupied significant areas of grassland and displaced native herbaceous species. Using fire to maintain open grassland may result in more native herbaceous cover remaining in place.

Introduction

Woody plant encroachment into open grasslands occurs worldwide and brings with it a host of ecological and management impacts: loss of grassland habitat and species, changes in ecosystem attributes and services, increased fuel loading, loss of forage for grazing animals, and decreased recreational

opportunities (Naito & Cairns 2011; Archer & Predick 2014). Disruption of disturbance regimes, such as fire, plays an important role in shrub encroachment (Archer et al. 2017), and reduced fire frequency is an important cause of woody encroachment into grassland (Twidwell et al. 2016). Prescribed fire is often used in attempts to restore grassland habitat; however, the ability of many shrub species to survive fire and subsequently resprout can significantly limit the efficacy of fire as a grassland restoration tool (Dacy & Fulbright 2009; Fuhlendorf et al. 2011; Keeley et al. 2012; Clarke et al. 2013; Twidwell et al. 2016). Past work reviewing the role of prescribed fire in controlling shrubs found that resprouting shrubs typically recovered to nonburned densities within 3 years, suggesting that

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single prescribed burns cause little or no mortality of resprouting shrubs (Fuhlendorf et al. 2011).

Along the central coast of California, U.S.A., shrub encroachment is converting grasslands into shrub-dominated communities. The native asteraceous shrub, *Baccharis pilularis* (coyote brush), is of major concern as its encroachment into the region's grasslands has occurred for at least half a century, in part because livestock grazing and fire have declined on the urbanizing landscape of the central coast (Clarke 1959; McBride & Heady 1968; Russell & McBride 2003; Ford & Hayes 2007). Northern coastal scrub, of which *B. pilularis* is a dominant species, and coastal prairie typically intergrade, forming a continuum that ranges from dense shrub cover to open grassland (Ford & Hayes 2007). Wind-borne *B. pilularis* seed can readily disperse to open grassland and establish, especially in years with wet springs (da Silva & Bartolome 1984; Williams et al. 1987).

Once *B. pilularis* has established in grassland, herbaceous species, including native grasses, decline significantly in biomass and reproductive output (Hobbs & Mooney 1986). Ecosystem conditions, such as nitrogen cycling, biomass and soil carbon storage, and soil moisture, can also change, potentially impeding reestablishment of coastal prairie (Zavaleta & Kettley 2006). Halting *B. pilularis* encroachment and restoring shrub-dominated areas to grassland are important objectives for many land managers along California's coast.

Additionally, although the negative impacts of shrub encroachment are clear, land managers need information about potential impacts of shrub reduction activities, such as burning, on other species, in particular native herbaceous species and invasive species (DiTomaso et al. 2013; Wonkka et al. 2017). Native perennial grasses in the coastal prairie are of particular concern and have shown variable responses to fire (D'Antonio et al. 2002). In addition, one invasive annual grass present on the study site, *Brachypodium distachyon* (purple false brome), is of particular interest to managers as very little is known about its control (Cal-IPC 2003). Information about the effect of fire on this invasive grass would be of interest to land managers in California, Chile, and Australia, where the species is known to be invasive (PIER 2011).

Although cattle can help maintain existing shrub-grassland boundaries by trampling and desultory grazing on shrub seedlings (McBride & Heady 1968), once a stand of *B. pilularis* has established, cattle grazing is of limited use in eliminating the shrubs in favor of grassland species. A single prescribed burn does not generally restore coastal prairie effectively because many shrubs, including *B. pilularis*, are able to resprout following a fire and quickly reestablish preburn cover (Ford & Hayes 2007; Fuhlendorf et al. 2011).

Two strategies have been proposed to address the challenge of resprouting shrubs, both with the aim of raising shrub mortality levels: (1) increasing fire intensity or (2) conducting consecutive burns. Increasing the intensity of prescribed burns may result in greater shrub mortality (Moreno & Oechel 1991; Keeley 2006; Smit et al. 2016; Twidwell et al. 2016), but such fires may increase impacts on nontarget species and be difficult to implement and safely control, especially in wildland–urban interface zones. Burning in consecutive years might be a

preferred alternative in many instances. Newly resprouting shrubs may be more vulnerable to repeat disturbance (Paula & Ojeda 2009; Enright et al. 2011; Ratajczak et al. 2014a), resulting in higher mortality rates after a second prescribed burn (Zedler et al. 1983). Although many woody basal-resprouting species store more nonstructural carbohydrates than are needed for a single resprouting event, two consecutive fires may completely drain these carbohydrate reserves before they can be replenished (Clarke et al. 2013). For example, a prior study in California found some limited evidence that, in contrast to a single burn, fire in two consecutive years might cause higher *B. pilularis* mortality (Havlik 1984).

Our objectives for this study were twofold: (1) we tested the hypothesis that two consecutive prescribed burns would increase shrub mortality, and (2) we sought to detect additional benefits or negative impacts to the herbaceous community of two consecutive burns.

Methods

Study Area

Our study site was located in the Point Pinole Regional Shoreline, part of the East Bay Regional Park District (EBRPD), on the northeastern coast of the San Francisco Bay, California, U.S.A. All plots were within 1 km of the bay. Vegetation was primarily coastal prairie grassland, with stands of the native shrub *Baccharis pilularis* interspersed, and with a significant component of naturalized or invasive nonnative herbaceous plants. Herbaceous biomass ranged from approximately 2,000–4,000 kg/ha. One native bunchgrass, *Stipa pulchra* (purple needlegrass), was abundant at the site (7–43% cover) and dominant in some locations. A second native bunchgrass, *Danthonia californica* (California oatgrass), and a rhizomatous, native perennial grass, *Elymus triticoides* (creeping wildrye), were also present at lower levels. *Festuca perennis* (Italian ryegrass) and *Avena* spp. (wild oats), common, naturalized annual grasses in the region, were abundant, and we identified several areas of the invasive *Brachypodium distachyon* on the site. Some, if not all, of the study site was subject to significant disturbance in the previous century from nearby industrial activities. Sheep and goat grazing is used as a vegetation management tool at the study site, but livestock grazing did not occur on our plots during the study.

The Bay Area has a Mediterranean maritime climate, characterized by mild, wet winters and warm, dry summers. Temperatures are moderate, and rain falls mainly in the winter, with very little precipitation from June through September. Average annual rainfall is approximately 56 cm, although summer fog drip provides significant additional moisture; annual mean minimum temperature in January is 5.5°C, and annual mean maximum temperature in July is 22°C (Kelch & Murdock 2012). Starting in 2012, an unprecedented 4-year drought occurred in California (Robeson 2015); the drought likely affected vegetative cover, especially of annual grasses, in the final year of this study.

Experimental Design

To assess consecutive fire effects on *B. pilularis* stands and the herbaceous community, we randomly sited 10 plot pairs and randomly assigned burn treatments to 5 of the plot pairs. Each plot pair included a shrub-dominated plot (shrub plots) with greater than 20% shrub cover (ranging from 20–64% cover) based upon visual inspection, and an adjacent herbaceous-dominated plot with visible native bunchgrass presence (herbaceous plots). Unburned control plots were protected from fire by mowlines and blacklines. Each plot in a plot pair was approximately 400 m².

Vegetation Sampling

We collected vegetation data for four years in June or July of 2009–2012. In the burn years (2009 and 2010), we collected data before the fire treatment was implemented. We measured shrub and herbaceous aerial cover (sensu Fehmi 2010) with permanent, 10-m line-point transects that were randomly located in each of the 20 plots. We recorded the species or other item (soil, rock, dead biomass) that was first intercepted from above with a point at every 20 cm along the transect for a total of 50 data points per transect. We use absolute percent cover in our descriptive analyses, defined as the number of positive point intercepts of a species divided by the total number of point intercepts taken, including samples that intercepted soil, rock, or litter.

In 2009, we tagged 25 randomly selected *B. pilularis* individuals in each of the 10 shrub plots (total of 250 individual shrubs) and relocated these individuals in 2010–2012. For each tagged shrub, we recorded: (1) whether it was alive or dead (defined as the absence of visible aboveground live tissue, including resprouts), (2) whether, if dead, it appeared to have been killed by fire (e.g. black scorch marks on dead stems; absence of aboveground biomass), and (3) whether, if alive, the shrub had resprouted. We were unable to relocate 10 of the 250 *B. pilularis* tags we deployed. In these cases, using a sub-meter accuracy GPS unit (Trimble GeoXH), we searched the area around the individual shrub's GPS coordinates. If we could find no living *B. pilularis* within a 1-m radius of the coordinates, we assumed for the purposes of analysis that individuals in burned plots were dead and had been killed by fire. If a living *B. pilularis* was found within a 1-m radius but no tag was found, we censored that individual from the survival analysis.

Prescribed Burns

The first prescribed burn occurred on 29 October, 2009. Although we did not directly measure fire intensity, the intensity was lower than desired because rainfall shortly before the fire produced newly germinating green grass and increased fuel moisture. The fire had patchy coverage and burned slowly through the previous year's thatch with flame lengths under 30.5 cm.

The second burn occurred on 2 days, 31 August and 21 September, 2010. Ample, dry fuel resulted in a higher intensity fire than the previous year's, with flame lengths reaching

heights of approximately 4 m. See Tables S1 and S2 for weather data for the fire dates.

Analysis

We analyzed response to burning for the shrub species of interest, *B. pilularis*, and six grasses: *S. pulchra*, *D. californica*, *E. triticoides*, *B. distachyon*, *F. perennis*, and *Avena* spp. For each species of interest, we tested for differences in cover by burn treatment, plot, vegetation type (shrub or herbaceous dominated), year (as a categorical variable), and an interaction between burn and year. We used a generalized linear mixed-effects model that included plot as a random effect (as a random intercept and fixed mean) to account for lack of independence in the residuals due to repeated measures of the plots (Laird & Ware 1982). We modeled the effects using the binomial distribution and a logit link function as described in the following equation, where π is the probability of the occurrence of the species of interest (Table 1):

$$\text{logit}(\pi_{ijk}) = \eta + \text{Burn}_i + \text{VegType}_k + \text{Year}_l + \text{Burn} : \text{Year}_{il} + (1 | \text{Plot}_j).$$

This model was unable to converge for assessing the occurrence of *D. californica* and *F. perennis* so, for these two species, we removed the interaction term to simplify the model to reach convergence (Table 2):

$$\text{logit}(\pi_{ijk}) = \eta + \text{Burn}_i + \text{VegType}_k + \text{Year}_l + (1 | \text{Plot}_j).$$

To test for significance of shrub mortality in burn treatments, we performed a survival analysis that included censoring of individual shrubs where tags could not be relocated and we could not determine mortality status. We used the Kaplan–Meier method and log-rank test to assess whether the survival curves of the burned and unburned shrubs differed significantly. We calculated life tables to estimate hazard, or the estimated risk of death in a given time interval.

Results

Of the seven species we analyzed, we found significant effects of fire on two: the shrub, *Baccharis pilularis* (negative,) and a naturalized annual grass, *Avena* spp. (positive). Our analysis also revealed strong interannual effects on all species except the native perennial grasses, *Danthonia californica* and *Elymus triticoides*. We found significant differences in cover between shrub and herbaceous plots for all herbaceous species except the invasive annual grass, *Brachypodium distachyon* (Tables 1 & 2).

Baccharis pilularis Cover

Before the first burn, there was no statistical difference in *B. pilularis* cover between the shrub-dominated plots selected for the burning treatment (28%) and the unburned control plots (37%; two-tailed *t* test, *p* value = 0.37). On unburned plots, *B. pilularis* cover increased at an average of 5.7% per

Table 1. Results of a generalized linear mixed-effects model for the response of five species of interest to the independent variables of year, burning, shrub/herbaceous plots, and an interaction between burn and year. Asterisks show statistically significant differences: ** $p < 0.05$; *** $p < 0.01$.

| | Dependent variable | | | | |
|--------------------------------|----------------------------|----------------------|---------------------------|--------------------|--------------------------------|
| | Baccharis pilularis (1) | Stipa pulchra (2) | Elymus triticoides (3) | Avena spp. (4) | Brachypodium distachyon (5) |
| 2010 | 0.17 (0.2) | 0.36** (0.17) | -0.7 (1.23) | 0.18 (0.2) | 0.39** (0.19) |
| 2011 | 0.92*** (0.19) | 0.27 (0.17) | -15.86 (33.82) | -1.2*** (0.28) | 0.17 (0.2) |
| 2012 | 1.02*** (0.19) | 0.66*** (0.16) | -15.83 (44.15) | -1.77*** (0.34) | 0.76*** (0.18) |
| Burned | -0.36 (0.58) | -0.01 (0.4) | 0.75 (1.1) | 0.32 (0.51) | 0.14 (0.76) |
| Shrub plots | 3.76*** (0.19) | -1.51*** (0.09) | 3.99*** (1.01) | 0.54*** (0.11) | 0 (0.09) |
| 2010: Burned | -1.32*** (0.32) | -0.38 (0.24) | 1.65 (1.37) | -0.02 (0.27) | 0.1 (0.26) |
| 2011: Burned | -2.61*** (0.35) | -0.27 (0.24) | 17.38 (33.83) | 1.99*** (0.33) | -0.34 (0.27) |
| 2012: Burned | -1.34*** (0.29) | 0.02 (0.23) | 17.35 (44.16) | 1.17*** (0.4) | 0.09 (0.25) |
| Constant | -4.49*** (0.45) | -1.06*** (0.28) | -9.21*** (1.34) | -2.63*** (0.37) | -2.35*** (0.54) |
| Observations | 4,000 | 4,000 | 4,000 | 4,000 | 4,000 |
| Log likelihood | -1.1e + 03 | -1.8e + 03 | -2e + 02 | -1.3e + 03 | -1.6e + 03 |
| Akaike information criterion | 2.3e + 03 | 3.7e + 03 | 4.3e + 02 | 2.5e + 03 | 3.3e + 03 |
| Bayesian information criterion | 2.4e + 03 | 3.7e + 03 | 4.9e + 02 | 2.6e + 03 | 3.4e + 03 |

year, while on burned plots, cover decreased at a rate of -1.9% per year, resulting in a significant reduction by the prescribed fire treatments (Table 1; Fig. 1). The model revealed highly

Table 2. Results of a generalized linear mixed-effects model for the response of *Danthonia californica* and *Festuca perennis* to the independent variables of year, burning, and shrub/herbaceous plots (interaction term for burn and year were not included in the model as in Table 1 due to lack of convergence). Asterisks show statistically significant differences: ** $p < 0.05$; *** $p < 0.01$.

| | Dependent Variable | |
|--------------------------------|-----------------------|--------------------|
| | D. californica (1) | F. perennis (2) |
| 2010 | 0.48 (0.45) | -0.41** (0.16) |
| 2011 | -0.43 (0.54) | -0.44*** (0.16) |
| 2012 | 0.56 (0.44) | -1.72*** (0.22) |
| Burned | 0.08 (4.19) | 1.2 (1.05) |
| Shrub plots | -1.45*** (0.38) | -0.74*** (0.13) |
| Constant | -12.83*** (3.92) | -3.09*** (0.76) |
| Observations | 4,000 | 4,000 |
| Log likelihood | -1.7e + 02 | -8.9e + 02 |
| Akaike information criterion | 3.4e + 02 | 1.8e + 03 |
| Bayesian information criterion | 3.9e + 02 | 1.8e + 03 |

significant negative year and burn interaction effects ($p < 0.01$) for every subsequent year compared to baseline conditions in 2009 (Table 1). In 2010, following the first burn treatment, average *B. pilularis* cover on burned treatment plots decreased to 10%, while unburned control plot average cover increased from 37 to 40% (Table S3; Fig. 1). In 2011, following the second prescribed burn, average cover of *B. pilularis* on burn treatment plots decreased to 7%, while average cover of *B. pilularis* on unburned control plots increased to 52% (Fig. 1). At the end of the study, 2 years after the second prescribed burn, average cover of *B. pilularis* on burn treatment plots recovered to 22%, and average cover of *B. pilularis* on unburned control plots continued to increase to 54% (Fig. 1).

Plot-scale differences in slope and soil moisture appeared to cause variation in burn impacts among plots. One plot in a flat area (PP3; Fig. 1) experienced the least reduction in *B. pilularis* cover, and another plot located in a swale (PP4; Fig. 1) recovered very quickly after the fire. Plots on steeper slopes experienced a greater reduction in cover and slower recovery (PP7 and PP5; Fig. 1).

In the preburn year, 2009, *B. pilularis* occurred at negligible cover in the herbaceous plots (Table S5). Over the four years of the study, the shrub increased in the unburned herbaceous plots from <1 to >6% cover to become the species with the third highest cover, whereas it did not occur in the burned herbaceous plots (Table S5).

Baccharis pilularis Mortality

The hazard, or estimated risk of mortality to burned shrubs in a given year, increased from 20.2% (95% confidence interval

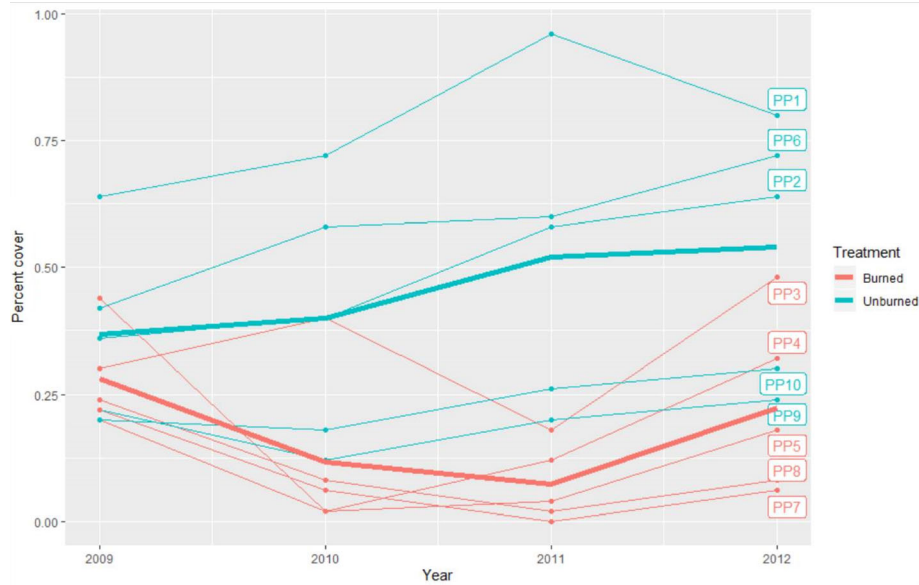


Figure 1. *Baccharis pilularis* absolute percent cover by treatment, in burned and unburned shrub plots in Point Pinole Regional Shoreline, California, 2009–2012. Burns occurred after data collection in 2009 and 2010. Thin lines represent individual plots; thick lines averages for each treatment type.

[CI]: 13.1–27.2%) after the first fire to 35.7% (95% CI: 26.2–45.2%) after the second fire (Fig. 2). After the first burn, 80% (95% CI: 73.3–87.3%) of burned shrubs survived, while 96.8% (95% CI: 93.8–99.9%) of unburned shrubs survived. After the second burn, 51.4% (95% CI: 43.3–61.1%) of the cohort of tagged *B. pilularis* still survived, while 94.2% (95% CI: 90.2–98.5%) survived in the unburned plots (Fig. 2).

As with *B. pilularis* cover, plot-scale differences in slope and soil moisture appeared to cause variation in mortality among plots. Mortality at the plot level after the first burn varied from

0–52%, and after the second burn from 28 to 80%. Individuals in plots on steeper slopes (PP5 and PP7) suffered much higher mortality levels.

Native Perennial Grass Cover

We did not find any statistically significant effects of burning or year/burn interaction effects on the three native perennial grasses, *Stipa pulchra*, *Danthonia californica*, and *Elymus triticoides* (Tables 1 & 2). *S. pulchra* was the most abundant species overall on the herbaceous plots in all four years, ranging from 24 to 44% cover (Table S5; Fig. 3). Although we did not detect an effect of fire, we found statistically significant interannual variation in *S. pulchra*, as it increased significantly in 2010 and 2012 compared to the 2009 baseline (Table 1; Fig. 3). The species also had significantly lower values on shrub plots compared to herbaceous plots (Table 1). *D. californica* occurred on only three plots over the course of the study (Table S4) and was significantly lower on shrub plots compared to herbaceous plots (Table 2). Although we did not find a significant effect of burning (Table 2), *D. californica* cover increased on burned plots and decreased on unburned plots (Table S4; Fig. 3). Finally, *E. triticoides* did not exhibit any significant effects from fire or from interannual variation; however, it was present at significantly higher levels on shrub plots compared to herbaceous plots. We did see an increase in cover of *E. triticoides* on burned shrub plots between 2009 (1.6% cover) and 2012 (6.8% cover), but it was not significant (Table S3; Fig. 3).

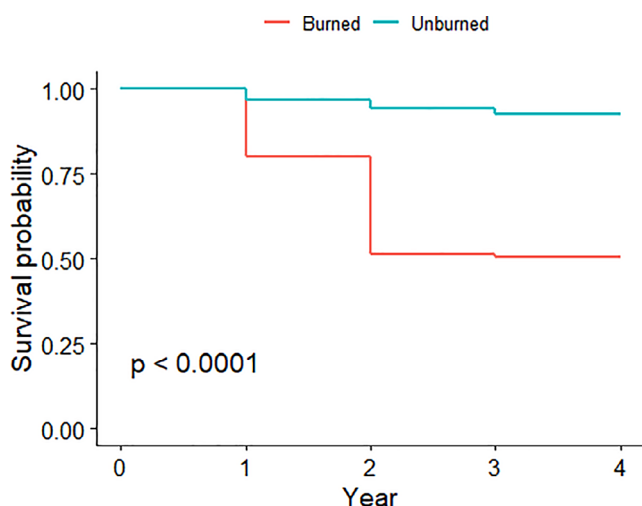


Figure 2. Survival probability of 250 *Baccharis pilularis* shrubs over four years in burned and unburned plots, Point Pinole Regional Shoreline, California, 2009–2012. Burns occurred after data collection in years 0 and 1.

Nonnative Annual Grass Cover

The three nonnative annual grasses we analyzed, *Avena* spp., *Festuca perennis*, and *B. distachyon*, were the most common

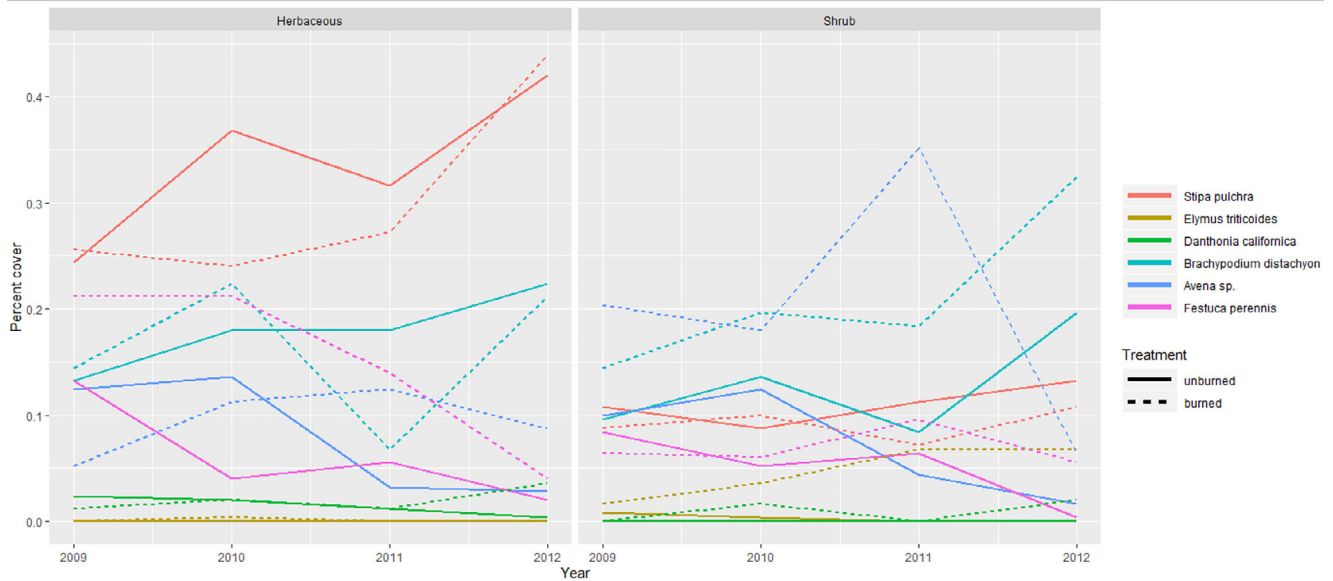


Figure 3. Herbaceous plant species absolute percent cover by burn treatment in herbaceous (left) and shrub (right) plots in Point Pinole Regional Shoreline, California, 2009–2012. Burns occurred after data collection in 2009 and 2010.

nonnative herbaceous species in the study area. Of the three, *Avena* spp. was the only species exhibiting a significant year and burn interaction effect, with greater cover on burned plots in 2011 and 2012 compared to the 2009 baseline (Table 1). We found significant interannual variation in the cover of these three nonnative species that was not attributable to fire: *Avena* spp. experienced declines in 2011 and 2012 compared to 2009; *F. perennis* had consistently lower cover each year after 2009; and *B. distachyon* had significantly higher values in 2010 and 2012 compared to 2009 as the invasive grass generally increased on both burned and unburned plots throughout the study (Tables S3 & S5; Fig. 3).

Discussion

Our results demonstrated that two consecutive burns reduced cover and increased mortality of *Baccharis pilularis*, while having minimal impacts on other herbaceous species of concern. Two years after the second burn, *B. pilularis* cover on burned plots was only 41% of the cover on unburned plots. We also found that shrubs quickly recovered over time, consistent with the work of Ratajczak et al. (2014b) in more mesic tallgrass prairie in Kansas, U.S.A., which found annual burns limited shrub encroachment, while longer burn intervals resulted in increased shrub cover. Only one herbaceous species, *Avena* spp., showed a significant impact from fire (positive).

Our study found supporting evidence that shrub encroachment into grassland changes vegetation structure and species composition, as the shrub plots had significantly different cover values for all but one of the herbaceous species tested. This shrub encroachment likely contributes to previously documented ecological and management impacts, including grassland habitat loss, increased fuel loading, and changes in ecosystem

attributes and services (Hobbs & Mooney 1986; Russell & McBride 2003; Zavaleta & Kettley 2006; Eldridge et al. 2011; Archer & Predick 2014; Stanton et al. 2018). These changes can occur rapidly, as we found shrub cover increased in the absence of fire and grazing by 5.7% per year, in accordance with another study in the central coast of California that found type-conversion from grassland into shrub-dominated communities within 15 to 25 years (Ford & Hayes 2007).

Highly variable mortality rates between our plots suggest that spatial variation in topography and soil moisture also likely play a key role in shrub mortality and recovery after fire. One flat plot did not experience high mortality, while a plot in a wetter swale experienced rapid recovery. We found control to be greatest on slopes, where flame heights and intensity were increased. Ratajczak et al. (2017) similarly observed site variation in tall-grass prairie susceptibility to shrub encroachment and posited that differences in site factors such as soils, water-holding capacity, and topography resulted in variability in woody encroachment.

Average *B. pilularis* mortality following the first prescribed burn was 22% in the burned plots, which is similar to or slightly higher than the mortality rates observed in a prior study in California coastal grasslands (Havlik 1984). Our 51% mortality result after two burns is considerably less than the 83% mortality observed by Havlik (1984) in his twice-burned site, which could be attributable to the low intensity of our first burn.

In some studies, increased fire frequency has not provided effective control of woody species. Higgins et al. (2007) found that fire frequency did not influence density of woody plants in a South African savanna. In Missouri, U.S.A., grasslands, implementation of prescribed burning on 3–6-year rotations slowed but did not reverse woody encroachment (Miller et al. 2017). In response, several research groups have investigated

the efficacy of increasing the intensity rather than the frequency of fire and have reported good control of resprouting woody species using intense fires to increase mortality (Higgins et al. 2007). Smit et al. (2016), working in South African savannas, and Twidwell et al. (2016), working in Texas, U.S.A., shrublands, both reported that high-intensity fires were effective in reducing woody encroachment. Their studies took place in large protected areas or an experiment station, locations that allowed for burning in conditions that caused “extreme fire behavior” (Twidwell et al. 2016). Although high-intensity fire may be effective in many places, it may not be permitted or feasible in wildland-urban interface zones (Smit et al. 2016; Miller et al. 2017). In addition, native herbaceous species of conservation concern may be killed by high-intensity fires (Miller et al. 2017) but are likely to survive lower-intensity burns (Wonkka et al. 2017). These factors suggest that the approach of two consecutive lower-intensity fires demonstrated in this study might expand the toolbox for land managers seeking to limit shrub encroachment.

The potential for effective use of consecutive fires is limited in some ecosystems by inadequate fuel accumulation over the intervening year to carry the second fire (Smit et al. 2016). In Missouri grasslands, Miller et al. (2017) found that woody plants reinforced their dominance and inhibited reestablishment of open grassland by shading out herbaceous plants, thereby reducing fine fuels and, thus, intensity of subsequent fires. Ratajczak et al. (2014b) reported similar dynamics in Kansas tallgrass prairie. This may be a particular problem in arid ecosystems with limited herbaceous fuels. In the semi-arid grassland systems of California, nonnative annual grasses generally provide abundant fine fuels every year (Spiegel et al. 2016). However, in large, well-established shrub stands with limited herbaceous understory, fine fuel loading sufficient for a second burn may be an obstacle to implementing the consecutive fire approach (Hobbs & Mooney 1986).

Interannual effects were the most common significant effect for all the species, except for the two sparsely distributed perennial grasses, *Danthonia californica* and *Elymus triticoides*. California grassland composition is known to be driven to a significant degree by highly variable annual weather patterns (Jackson & Bartolome 2002). This study confirms this finding as annual effects such as weather resulted in more significant changes to the herbaceous community than fire.

A concern about use of intense fire, and prescribed fire in general, is its impact on native herbaceous species of conservation interest (Miller et al. 2017; Wonkka et al. 2017). In our study, native herbaceous species did not show significant responses to the two burns. Although the trends were not statistically significant, we did see increasing cover of *D. californica* and *E. triticoides* on burned plots and decreasing cover on unburned plots (Fig. 3). Consistent with our results, previous studies found that *S. pulchra* responded variably to fire, and that *D. californica* did not change significantly with late summer burning (although *D. californica* has been shown to decrease with early summer burning) (Hatch et al. 1999; D’Antonio et al. 2002). These results concur with those of Wonkka et al. (2017), who also found that low-intensity fire in southwest Texas, U.S.A.,

resulted in perennial grass mortality rates similar to those in untreated control plots.

Brachypodium distachyon, the invasive, annual grass weed, was one of the most abundant herbaceous species in our study. In contrast to all the other herbaceous species, *B. distachyon* cover did not differ between shrub- and herbaceous-dominated plots. Over the four years of the study, it increased between 50 and 130% in the shrub and herbaceous plots, both burned and unburned; therefore, the increase was unlikely to have resulted from the prescribed burns. Both fires occurred in late summer/early fall, after most annual grass seed had detached from the parent plant and was protected in the soil. Burns earlier in the season, targeted to kill grass seeds while still elevated above ground on the culm, may be a more effective form of control for this invasive grass (Reiner 2007; DiTomaso et al. 2013). However, *D. californica*, one of the site’s native perennial grasses, has been shown to decline substantially following early summer burns (D’Antonio et al. 2002). Because of such inherent conflicts, prescribed burns with multiple objectives, like those of this study, need to prioritize objectives when choosing burn season, intensity, and other factors (Miller et al. 2017).

Herbaceous dicots often increase following fire in California grasslands (D’Antonio et al. 2002; Reiner 2007). The nonnative annual mustard, *Brassica nigra* (black mustard), is known to invade after fire (DiTomaso et al. 2013); however, we only detected this species twice before the burns and did not observe it thereafter (Table S3) so our study plots did not experience a *B. nigra* invasion following the prescribed fires.

Our results suggest that the nonnative grasses, *Avena* spp. and *Brachypodium distachyon*, occupied the space vacated by *Baccharis pilularis* in the two years after the prescribed burns. Native perennial grasses, although apparently not negatively impacted by the fire, did not immediately benefit from the fire by significantly increasing the space they occupied. Hobbs and Mooney (1986) found that nonnative annual grasses dispersed far more seed than native *S. pulchra*. Consequently, establishment of *S. pulchra* and other native perennial grasses into newly restored open grassland may take several years at a minimum, a period during which nonnative annual grasses are likely to remain dominant.

Another potential constraint on restoration of native grasses following shrub control is ecosystem changes that occur when woody vegetation occupies a site. Zavaleta and Kettley (2006) found that soil pH, total soil carbon, total soil nitrogen, and soil moisture increased with time after *B. pilularis* establishment in grassland. Even after the removal of *B. pilularis*, changes in soil nutrients and moisture may favor nonnative annual grasses, at least initially (Stromberg & Griffin 1996; Gea-Izquierdo et al. 2007), although further research would provide greater insight into this dynamic.

As described above, our study was limited by the low intensity of the first fire, which likely contributed to limited control after the first burn year, and may also be a confounding factor in the increased hazard rate and mortality we found after the second burn. Determining the fire intensity that reliably kills *B. pilularis* would help in developing more nuanced fire prescriptions in spatially variable landscapes. Although we did

not use pyrometers (e.g. Wally et al. 2006; Beckstead et al. 2011; Twidwell et al. 2016) in this study, we believe they would be useful in determining effective fire intensity for maximizing *B. pilularis* mortality while limiting impacts on native herbaceous species.

Restoration Recommendations

Fire can be an effective tool for long-term maintenance of coastal prairie, but its use is required relatively regularly to achieve desired results. Two years after the second prescribed burn, average cover of *B. pilularis* on burn treatment plots was returning to preburn levels, suggesting that frequent burns may be needed to reduce cover. Prescribed fire appeared to keep shrubs from establishing in herbaceous-dominated plots over the course of the study, indicating that fire may keep *B. pilularis* from establishing in open grassland in the first place.

Managers and land owners wanting to restore coastal prairie with fire following *B. pilularis* encroachment may increase shrub mortality if they can achieve at least two consecutive annual burns. Control may also be more effective in steeper, drier locations. In general, we recommend burning before shrubs have occupied large areas of grassland, displaced native herbaceous species, changed ecosystem conditions, and inhibited the herbaceous understory necessary to carry a second fire (Miller et al. 2017). Using fire to preserve open grassland may result in more native herbaceous cover remaining in place, in contrast to burning mature shrub stands and then hoping that native herbaceous species will rapidly reoccupy the site.

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LITERATURE CITED

- Archer SR, Predick KI (2014) An ecosystem service perspective on brush management: research priorities for competing land-use objectives. *Journal of Ecology* 102:1394–1407
- Archer SR, Andersen EM, Predick KI, Schwinning S, Steidl RJ, Woods SR (2017) Woody plant encroachment: causes and consequences. Pages 25–83. In: Briske DD (ed) *Rangeland systems: processes, management and challenges*. Springer, Cham, Switzerland
- Beckstead J, Street LE, Meyer SE, Allen PS (2011) Fire effects on the cheatgrass seed bank pathogen *Pyrenophora semeniperda*. *Rangeland Ecology & Management* 64:148–157
- Cal-IPC (California Invasive Plant Council) (2003) Plant assessment form [for *Brachypodium distachyon*]. <http://www.cal-ipc.org/ip/inventory/PAF/Brachypodium%20distachyon.pdf>
- Clarke WC (1959) The vegetation cover of the San Francisco Bay Region in the early Spanish period. Master's thesis. University of California, Berkeley
- Clarke PJ, Lawes M, Midgley J, Lamont BB, Ojeda F, Burrows GE, Enright NJ, Knox KJE (2013) Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. *New Phytologist* 197:19–35
- Dacy EC, Fulbright TE (2009) Survival of sprouting shrubs following summer fire: effects of morphological and spatial characteristics. *Rangeland Ecology & Management* 62:179–185
- D'Antonio C, Bainbridge S, Kennedy C, Bartolome J, Reynolds S (2002) Ecology and restoration of California grasslands with special emphasis on the influence of fire and grazing on native grassland species. Report prepared for the David and Lucille Packard Foundation. University of California, Berkeley, California
- DiTomaso JM, Kyser GB, Oneto SR, Wilson RG, Orloff SB, Anderson LW, et al. (2013) Weed control in natural areas in the Western United States. University of California Weed Research and Information Center, Davis, California
- Eldridge DJ, Bowker MA, Maestre FT, Roger E, Reynolds JF, Whitford WG (2011) Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. *Ecology Letters* 14:709–722
- Enright NJ, Fontaine JB, Lade JC, Miller BP, Westcott VC (2011) Fire interval effects on persistence of resprouter species in Mediterranean-type shrublands. *Plant Ecology* 212:2071–2083
- Fehmi JS (2010) Confusion among three common plant cover definitions may result in data unsuited for comparison. *Journal of Vegetation Science* 21:273–279
- Ford LD, Hayes GF (2007) Northern coastal scrub and coastal prairie. Pages 180–207. In: Barbour MG, Keeler-Wolf T, Schoenherr AA (eds) *Terrestrial vegetation of California*. Third edition. University of California Press, Berkeley, California
- Fuhlendorf SD, Limb RF, Engle DM, Miller RF (2011) Assessment of prescribed fire as a conservation practice. Pages 75–104. In: Briske DD (ed) *Conservation benefits of rangeland practices: assessment, recommendations, and knowledge gaps*. United States Department of Agriculture, Natural Resources Conservation Service, Washington D.C.
- Gea-Izquierdo G, Gennet S, Bartolome JW (2007) Assessing plant-nutrient relationships in highly invaded Californian grasslands using non-normal probability distributions. *Applied Vegetation Science* 10:343–350
- Hatch DA, Bartolome JW, Fehmi JS, Hillyard DS (1999) Effects of burning and grazing on a coastal California grassland. *Restoration Ecology* 7:376–381
- Havlik NA (1984) Effects of urban-industrial land use on vegetation and flora in the Potrero Hills, Richmond, California. PhD dissertation. University of California, Berkeley
- Higgins SI, Bond WJ, February EC, Bronn A, Euston-Brown DIW, Enslin B, et al. (2007) Effects of four decades of fire manipulation on woody vegetation structure in savanna. *Ecology* 88:1119–1125
- Hobbs RJ, Mooney HA (1986) Community changes following shrub invasion of grassland. *Oecologia* 70:508–513
- Jackson RD, Bartolome JW (2002) A state-transition approach to understanding nonequilibrium plant community dynamics in Californian grasslands. *Plant Ecology* 162:49–65
- Keeley JE (2006) Fire severity and plant age in postfire resprouting of woody plants in sage scrub and chaparral. *Madrono* 53:373–379
- Keeley JE, Bond WJ, Bradstock RA, Pausas JG, Rundel PW (2012) *Fire in Mediterranean ecosystems: ecology, evolution and management*. Cambridge University Press, Cambridge, United Kingdom
- Kelch DG, Murdock A (2012) Flora of the Carquinez Strait Region, Contra Costa and Solano Counties, California. *Madrono* 59:47–108
- Laird NM, Ware JH (1982) Random-effects models for longitudinal data. *Biometrics* 38(4):963–974
- McBride J, Heady HF (1968) Invasion of grassland by *Baccharis pilularis* DC. *Journal of Range Management* 21:106–108
- Miller JED, Damschen EI, Ratajczak Z, Özdoğan M (2017) Holding the line: three decades of prescribed fires halt but do not reverse woody encroachment in grasslands. *Landscape Ecology* 32:2297–2310

- Moreno JM, Oechel WC (1991) Fire severity and herbivory effects on postfire resprouting of *Adenostoma fasciculatum* in southern Californian chaparral. *Oecologia* 85:429–433
- Naito AT, Cairns DM (2011) Patterns and processes of global shrub expansion. *Progress in Physical Geography* 35:423–442
- Paula S, Ojeda F (2009) Belowground starch consumption after recurrent severe disturbance in three resprouter species of the genus *Erica*. *Botany-Botanique* 87:253–259
- PIER (United States Forest Service, Pacific Island Ecosystems at Risk) (2011) *Brachypodium distachyon*. www.hear.org/pier/species/brachypodium_distachyon.htm (accessed 19 Dec 2019)
- Ratajczak Z, Nippert JB, Briggs JM, Blair JM (2014a) Fire dynamics distinguish grasslands, shrublands and woodlands as alternative attractors in the Central Great Plains of North America. *Journal of Ecology* 102:1374–1385
- Ratajczak Z, Nippert JB, Ocheltree TW (2014b) Abrupt transition of mesic grassland to shrubland: evidence for thresholds, alternative attractors, and regime shifts. *Ecology* 95:2633–2645
- Ratajczak Z, D’Odorico P, Nippert JB, Collins SL, Brunsell NA, Ravi S (2017) Changes in spatial variance during a grassland to shrubland state transition. *Journal of Ecology* 105:750–760
- Reiner RJ (2007) Fire in California grasslands. Pages 207–217. In: Stromberg MR, Corbin JD, D’Antonio CM (eds) *California grasslands: ecology and management*. University of California Press, Berkeley, California
- Robeson SM (2015) Revisiting the recent California drought as an extreme value. *Geophysical Research Letters* 42:6771–6779
- Russell WH, McBride JR (2003) Landscape scale vegetation-type conversion and fire hazard in the San Francisco Bay Area open spaces. *Landscape and Urban Planning* 64:201–208
- da Silva PG, Bartolome JW (1984) Interaction between a shrub, *Baccharis pilularis* subsp. *consanguinea* (Asteraceae), and an annual grass, *Bromus molis* (Poaceae), in coastal California. *Madroño* 31:93–101
- Smit IPJ, Asner GP, Govender N, Vaughn NR, van Wilgen BW (2016) An examination of the potential efficacy of high-intensity fires for reversing woody encroachment in savannas. *Journal of Applied Ecology* 53:1623–1633
- Spiegel S, Huntsinger L, Hopkinson P, Bartolome JW (2016) Range ecosystems. Pages 835–864. In: Mooney H, Zavaleta E (eds) *Ecosystems of California*. University of California Press, Oakland, California
- Stanton RA, Boone WW IV, Soto-Shoender J, Fletcher RJ Jr, Blaum N, McCleery RA (2018) Shrub encroachment and vertebrate diversity: a global meta-analysis. *Global Ecology and Biogeography* 27:368–379
- Stromberg MR, Griffin JR (1996) Long-term patterns in coastal California grasslands in relation to cultivation, gophers, and grazing. *Ecological Applications* 6:1189–1211
- Twidwell D, Rogers WE, Wonkka CL, Taylor CA Jr, Kreuter UP (2016) Extreme prescribed fire during drought reduces survival and density of woody resprouters. *Journal of Applied Ecology* 53:1585–1596
- Wally AL, Menges ES, Weekley CW (2006) Comparison of three devices for estimating fire temperatures in ecological studies. *Applied Vegetation Science* 9:97–108
- Williams K, Hobbs RJ, Hamburg SP (1987) Invasion of an annual grassland in northern California by *Baccharis pilularis* ssp. *consanguinea*. *Oecologia* 72:461–465
- Wonkka CL, West JB, Twidwell D, Rogers WE (2017) Grass mortality and turnover following core rangeland restoration practices. *Rangeland Ecology & Management* 70:290–300
- Zavaleta ES, Kettley LS (2006) Ecosystem change along a woody invasion chronosequence in a California grassland. *Journal of Arid Environments* 66:290–306
- Zedler PH, Gautier CR, McMaster GS (1983) Vegetation change in response to extreme events: the effect of a short interval between fires in California chaparral and coastal scrub. *Ecology* 64:809–818

Supporting Information

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

Table S1. Air temperature, relative humidity, wind direction, and speed at 4 times during the first prescribed burn, 29 October, 2009.

Table S2. Air temperature, wind direction, and speed at 4 times during the second prescribed burn, 31 August and 21 September, 2010.

Table S3. Shrub plots species absolute percent cover by treatment, Point Pinole Regional Shoreline, California, 2009–2012.

Table S4. *Danthonia californica* absolute percent cover on the three burned and unburned plots in which it occurred, Point Pinole Regional Shoreline, California, 2009–2012.

Table S5. Herbaceous plots species absolute percent cover by treatment, Point Pinole Regional Shoreline, California, 2009–2012.

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