Prescribed Fire Effects on Population Dynamics of an Annual Grassland ☆

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ABSTRACT

Medusahead (*Elymus caput-medusae* [L.] Nevski) is a highly damaging invasive annual grass in California rangelands. While it has been shown that prescribed fire can be a successful tool in controlling medusahead populations, fire treatments are not always successful. Given the sociological and economic constraints of prescribed fire use, it is critically important that we maximize likelihood of treatment success. We conducted experimental investigation of population dynamics of competing species from different functional groups: invasive annual medusahead, naturalized but forageable nonnative wild oat (*Avena* spp. Pott ex Link), and native perennial purple needlegrass (*Stipa pulchra* [Hitchc.] Barkworth). We observed population dynamics at the 1-m² scale before and after treatments of prescribed fire and seed-limitation (weed whipping in a 1-m buffer area). We asked 1) what is the role of seed dispersal from burn edges on subsequent medusahead population size? and 2) how do density and fecundity of the dominant species respond to fire? Results showed that 1) seed dispersal is an important factor in recovery dynamics and 2) wild oat fecundity significantly increases in the year after fire while medusahead and needlegrass fecundity seem minimally affected. Ultimately, managers should consider fire as a preferable first-entry tool and should thoroughly consider shape and size of planned burns, as well as what vegetation is present to play a role in post-treatment seed-dispersal dynamics.

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Introduction

Medusahead (*Elymus caput-medusae* [L.] Nevski) is one of the most damaging invasive plants in North American rangelands. More than 400 000 hectares of the western United States have been invaded by medusahead, and its range is increasing at an average rate of 12% per year (Duncan et al., 2009). An annual grass, medusahead propagates efficiently and can quickly approach densities of 1 000 to 2 000 plants per square meter after initial establishment (Mangla et al., 2011). Mature plants are unpalatable to livestock; in invaded areas, grazing capacity can be reduced by 75 − 90% (M. Hironaka, 1961). Medusahead invasion has also been shown to significantly reduce species richness and diversity on the landscape (Davies and Svejcar, 2008), an effect believed to lead to an overall reduction of ecosystem services (Walker et al., 1999).

Although most past research has shown that prescribed fire can reduce medusahead populations, some results have shown much less success (DiTomaso et al., 2007; Kyser et al., 2008). Given the environmental, social, and economic constraints on using prescribed fire (Quinn-Davidson and Varner, 2011), it is important to maximize its effectiveness if fire is to be a successful management tool. Understanding the effects of prescribed fire on key aspects of medusahead population dynamics and relative species densities will guide public and private land managers about more effective ways to efficiently improve rangelands. Previous research on fire effects on medusahead indicated that burns should be timed when seed heads are ripe and doughy but not yet dispersed (DiTomaso et al., 2005; Sweet, 2005). Because medusahead has a later seasonal phenology than other grassland species, carefully timed prescribed fire can expose medusahead seeds to maximum heat, after other species' seeds have already dropped, escaping the heat of the fire and remaining viable on the soil surface. However, even with this timing, burns are not always successful (Kyser et al., 2008). A hitherto unexplored factor that may influence the effectiveness of prescribed burns is burn size and the influence of treatment edges. If burns are conducted with high populations of medusahead surrounding burn edges, medusahead could quickly reinvade from burn edges even when the burn successfully treated medusahead within the burn. Another aspect needing more research is how the density of medusahead within the treatment unit affects fire impact. Finally, the postfire fecundity responses of rangeland focal species are also unknown.

We evaluated the recovery dynamics of an annual rangeland treated with prescribed fire targeting reduction of medusahead. Specifically, we address the following questions: 1) What is the role of seed dispersal from burn edges on subsequent medusahead population size? and 2) How do density and fecundity of the dominant species respond to fire? We expect a burn-edge interaction in burn plots with low initial within-plot medusahead populations and undisturbed medusahead presence in plot edges. This information can be applicable at larger

spatial scales to help guide decisions regarding how land managers approach medusahead management.

Methods

Study Area

The study was conducted at Sierra Foothills Research and Extension Center (SFREC), a University of California — owned property located 97 km northeast of Sacramento in Browns Valley, California (Fig. 1). The project site is an annual rangeland characterized by Mediterranean climate, with cool, wet winters and hot, dry summers. Weather data from the California Irrigation Management Information Systems station in Browns Valley shows that, since 1962, annual precipitation varies from 23–132 cm per year, with a mean of 71 cm, and air temperatures range from an average of 4°C minimum in winter and 32°C maximum in summer. Total precipitation during both years of the experiment was below average. Precipitation from September to May leading up to the experiment in 2013 totaled 52 cm, with most occurring in December 2012. Precipitation in the year following treatments totaled to 44 cm, with most occurring in February and March of 2014 (California Irrigation Management Information System). The soil is mapped as Sobrante-Timbuctoo Complex, primarily composed of a moderately deep and well-drained gravelly loam (Lytle, 1998). Cattle graze this

pasture site every year but for the 2 yr preceding this study were excluded from the project area.

Experimental Design and Data Collection

We studied population dynamics and prescribed fire treatment effects on three rangeland species dominants, their associated communities, and their interactions. These species were purple needlegrass (*Stipa pulchra* [Hitchc.] Barkworth) as a native perennial, wild oat (both *Avena barbata* and *Avena fatua;* hereafter grouped as *Avena* spp.) as a nonnative forage grass, and medusahead as a nonnative invasive species targeted for removal. These species were chosen because they are prevalent, high-abundance species on annual grasslands with high-impacts on rangeland ecosystems (DiTomaso et al., 1999, 2005, 2007; Kyser and DiTomaso, 2002; Blondel, 2003; Bartolome et al., 2007; Kyser et al., 2008; Sweet et al., 2008). Our study was conducted at small spatial scales (1 m²), focusing on the influence of edges, providing key insights that are scalable to the role of fire as a restoration tool in annual rangelands with similar species composition.

For project setup, 80 3 × 3 m experimental units were laid out in a grid and categorized into one of three categories by relative dominance of focal species: wild oat, needlegrass, or medusahead. Dominance was determined by ocular estimate of > 50% cover. Medusahead was present in every unit. Of these, 60 units were randomly selected for study—20
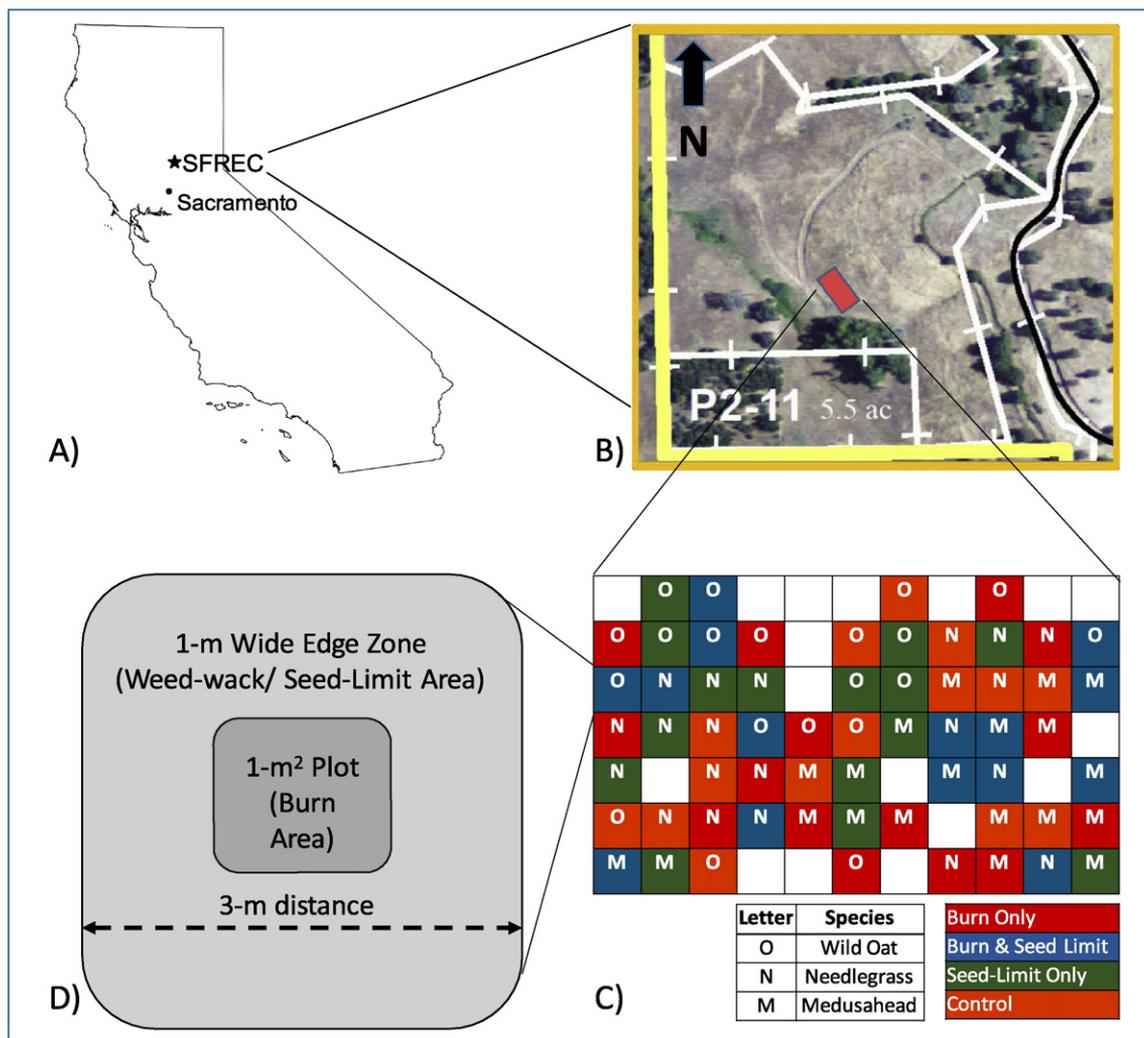
Figure 1. A, Location of study site at the Sierra Foothills Research and Extension Center (SFREC), Browns Valley, California. **B,** Expanded view of pasture at SFREC. Red block indicates study area. **C,** Layout of the experimental units—each color represents a different treatment, and each letter shows a different dominant species category pretreatment (O indicates wild oat; N, needlegrass; M, medusahead). **D,** Layout of experimental plot with 2 × 2 factorial design of treatments: burned or unburned and seed limited or not seed limited.

from each dominance category (O = wild oat−dominated units, N = purple needlegrass−dominated units, M = medusahead−dominated units) (Fig. 1C)−based on naming each unit within each category and using a randomizer in *Excel*. The center 1-square meter of each unit was designated as the fixed-area study plot; a 1-m−wide surrounding space was designated as the plot buffer to examine the influence of seed dispersal. Plots were split in a 2 × 2 factorial design: burned and unburned (1-m² burn boxes), seed limited (by cutting current year's growth in the 1-m plot buffer), and non-seed limited (Fig. 1D).

In May 2013, we measured pretreatment density and fecundity of the dominant grass, density of the other two focal species, and ocularly estimated percent cover of all species in every plot. Pretreatment percent cover was also collected for every species within a half meter distance on each side of the 1-m² plot; these data identified the species composition of most likely seeds dispersing into the plots posttreatment. Wild oat and medusahead density were measured in a 10 × 40 cm randomized subplot; needlegrass density was measured as number of bunches in the entire plot, as well as circumference of each individual bunch. Fecundity was measured for each of the three focal species according to highest correlation methods (Spotswood, unpublished data 2013); these correlated measurements were number of glumes, length of seedhead, and number of stalks for oat, medusahead, and needlegrass, respectively. Fecundity measurements were taken for 20 random individuals of each species per plot. All above measures were repeated exactly 1 yr posttreatment.

Burn and seed-limitation (cutting with a weed-whipper) treatments were implemented on plots according to treatment assignment the morning of 23 May 2013. Temperature was 24°C, and relative humidity ranged from 27–35%. Average wind speed was 5.6 kph with gusts of 13.7 kph from the South and Southwest. Soil average percent moisture and grass average percent moisture during the burn were 4.4% and 20.5%, respectively. All burn boxes were lit with a backing fire to consume all fine fuels. Burns were timed for the end of spring to best match existing recommendations for burning to control medusahead (Kyser et al., 2008). In plots used as controls for fire treatment, vegetation within the 1 m² was left intact. For seed-limitation treatments, a 1-m wide strip of the current year's growth was cut and removed on all four sides of the plots. For control plots of the limitation treatment, this 1-m−wide strip surrounding the center 1 m² was left intact as reseeding potential.

Immediately posttreatment, seed rain traps made from 8-cm diameter petri dishes spread with a thin layer of an adhesive insect glue were set. Nine were placed in each plot, distributed in a 3 × 3 grid pattern. These were left for the duration of the summer to estimate seed rain into the plot area posttreatment. In late September 2013, seed rain traps were collected and seeds were identified to species and counted.

Underneath the center seed rain trap we collected surface seeds, which consisted of seeds that fell into the plot soil surface pretreatment or were not consumed during the burn. Surface seeds were identified to species, tallied, and then planted in the greenhouse to determine germinability. This germination experiment was carried out in the Oxford Tract Greenhouse in Berkeley, California, from October 2012 to May 2013. Percent cover, fecundity, and stemcount measurements were taken again in May 2014 to assess change to plots posttreatment and better understand how plant and seed dynamics are linked in a management perspective.

Analytical Methods

Surface seeds collected and germinated in the greenhouse were analyzed for percent germinability across burn treatment. Medusahead seed rain into plots was tallied and compared across burn and seed-limiting treatments, as well as focal species' stem counts and fecundities. All tests were performed with analysis of variance (ANOVA) for preburn and postburn using *R* statistical software. Where significant differences occurred ($P < 0.05$), comparisons between means were

performed using Tukey's HSD multiple comparison test with the "agricolae" package in *R*. To account for random effects of unique plot baseline variations and for the effect of yearly variation, GLMER models run using the "poisson" statistical family were generated using *R*'s "lme4" package. This strengthened statistical outputs by isolating for fixed effects of treatments on focal species densities.

Shifts in plant vegetation types and indicator species were investigated using cluster analysis in PC-ORD (McCune and Mefford, 1999), which creates a dendrogram based on Bray-Curtis similarity values. Percent cover data were square-root transformed. Both community analyses based on percent cover data and stemcount analyses were analyzed and included because they approach the burn impact at different scales of effect. Community analyses look more generally at how plots shift or do not shift through time and what causes these changes or lack thereof. Stemcount analyses show the specific effect of the treatments on a subset of focal species densities.

Results

Treatment Effects on Seeds

First, we tested our hypothesis that the burn effectively reduced medusahead populations. Seeds collected from plot surfaces and germinated in the greenhouse estimated survivability of seeds after the prescribed fire treatment. Of the 425 medusahead seeds that were collected at the end of the summer, only 4 were germinable (.01%). This is compared with the germination rate from the control units, which was 182 out of 207 germinated (88%). Fire had less impact on wild oats, with 23 out of 89 (26%) germinating in the burn units and 65 out of 81 (80%) in the controls (Fig. 2). No needlegrass seeds were found in the germination experiment.

Medusahead seed rain in M plots was influenced by treatment (Fig. 3). Spread of seed-rain count data in unburned M plots was narrow compared with burned plots. Burned M plot seed-rain counts ranged from zero to well above those of unburned M plots. Highest seed-rain counts occurred in M plots that were burned but not seed limited. ANOVA showed that there were statistically significant differences across treatment groups. Seed-limited plots resulted in the lowest seed-rain counts ($P = 0.05$). Not treating plots (controls) resulted in a slightly higher seed-rain count than plots that were seed limited ($P = 0.05$), but these treatments were not significantly different from each other. Burning alone yielded the highest seed-rain counts ($P = 0.009$) and was in its own statistically significant group from other treatments. Burning combined with seed limitation fell into its own group with only slightly higher seed-rain counts than the control, but there was also less statistical confidence that this difference was due to more than random chance ($P = 0.089$).

Treatment Effects on Focal Species Density

ANOVA and Tukey's HSD was used to determine significance differences in medusahead densities across treatment groups before and after treatment (Fig. 4). Results indicate that treated groups were significantly different from groups that were not treated (both control and pretreatment). GLMER modeling medusahead stemcounts from all plots, with random effects of plot and year accounted for, found treated groups were distinct from controls ($P < 0.0001$). The mean expected baseline value for the control group was 19 stems. For this model, the seed-limit treatment group was not significantly different from the control. However, the burn-only group and the combination burn and seed-limit group were highly significantly different from the control, with ~8 fewer stems ($P < 0.0001$) and ~16 fewer stems ($P < 0.0001$) expected due to treatments, respectively. When running GLMER on medusahead stemcounts in M plots only, seed limit does become a treatment that is significantly different from the control with ~2 more stems expected due to seed limitation beyond the ~46 stem mean expected stemcount in the control group. GLMER results for treatment effects on medusahead
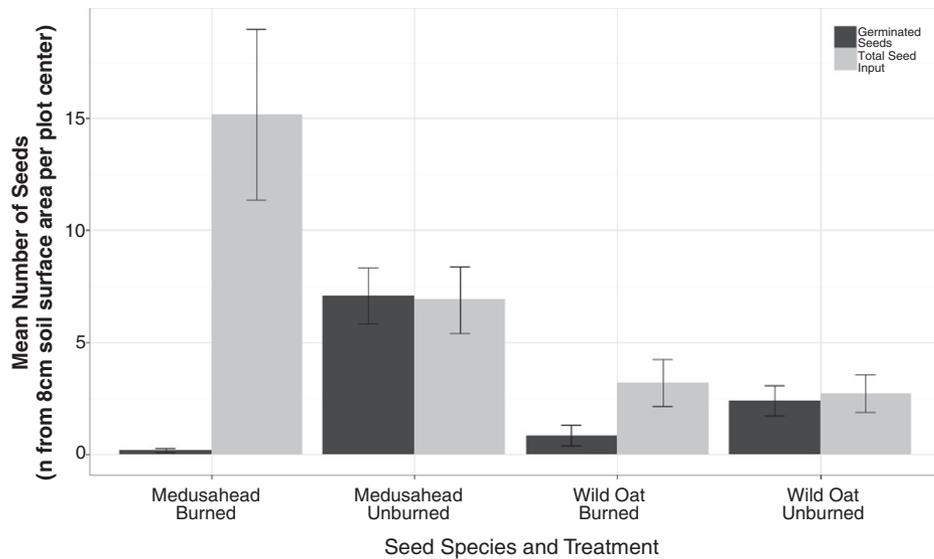
Figure 2. Mean per-plot surface seed germinability of medusahead and wild oat in burned versus unburned plot treatments (from 8-cm area at plot center). Treatment had a significant impact on medusahead germinability.

stemcounts in O and N plots were not as statistically significant but followed similar trends to models for all plots and M plots. GLMER results for treatment effects on needlegrass bunch counts and wild oat stemcounts showed that treatment was not a significant factor for difference from control groups ($P = 0.8155$ and $P = 0.399$, respectively).

Fecundity Responses to Treatments

Burning had a significant effect on wild oat and needlegrass fecundities but had no significant impact on medusahead fecundity (Fig. 5). The post-treatment standing crop fecundity for these two species was significantly different from year one's standing crop. Specifically, burning wild oat led to a significant increase in wild oat fecundity of an average five glumes higher than the control ($P = 0.015$). Needlegrass showed decreased fecundity from burning that was slightly statistically distinct from the unburned ($P = 0.069$).

Community Analysis of Vegetation Types and Drivers of Change

Analyses in PC-ORD resulted in determination of four vegetation types. Of these four pretreatment vegetation types identified, three of these had one clear indicator species: filaree (*Erodium* spp.), wild oat, and medusahead. The fourth vegetation type identified had multiple significant indicator species (needlegrass mix). The strongest indicator species in this vegetation type was needlegrass, but six others—four forbs and two grasses, all nonnative—were identified as significant species for community identification ($P < 0.05$) (Table 1). Three of these four vegetation types found through Bray Curtis community analysis matched the initial ocular dominance categorizations. The fourth, filaree, was not used as a dominance categorization because it was in the understory, and therefore less notably dominant in the first year, and because our study was focusing on dominant grasses. Community
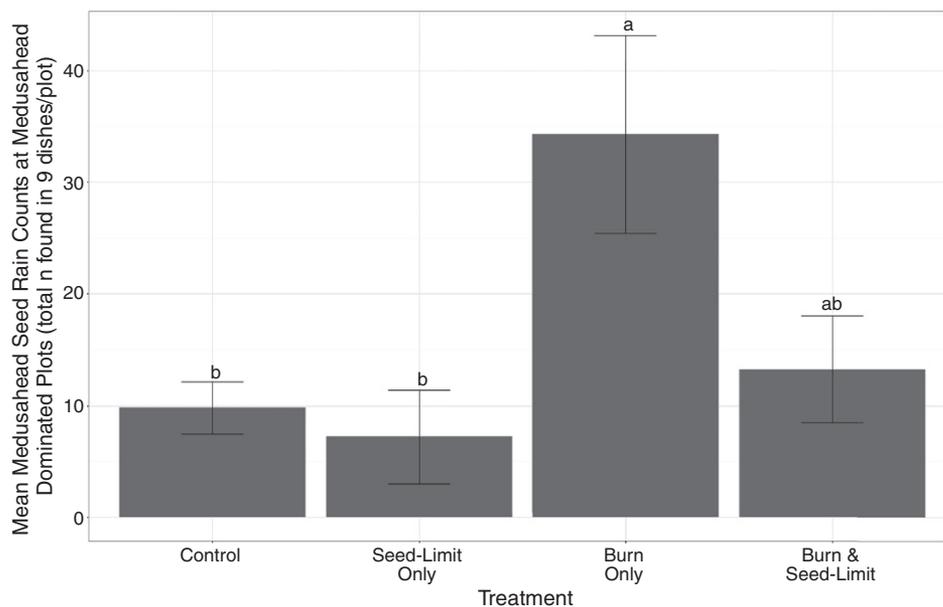
Figure 3. Effects of burning and edge removal on medusahead seed rain into nine 8-cm dishes per plot in medusahead −dominated plots. Analysis of variance results show that each treatment result was statistically significantly different from the control.
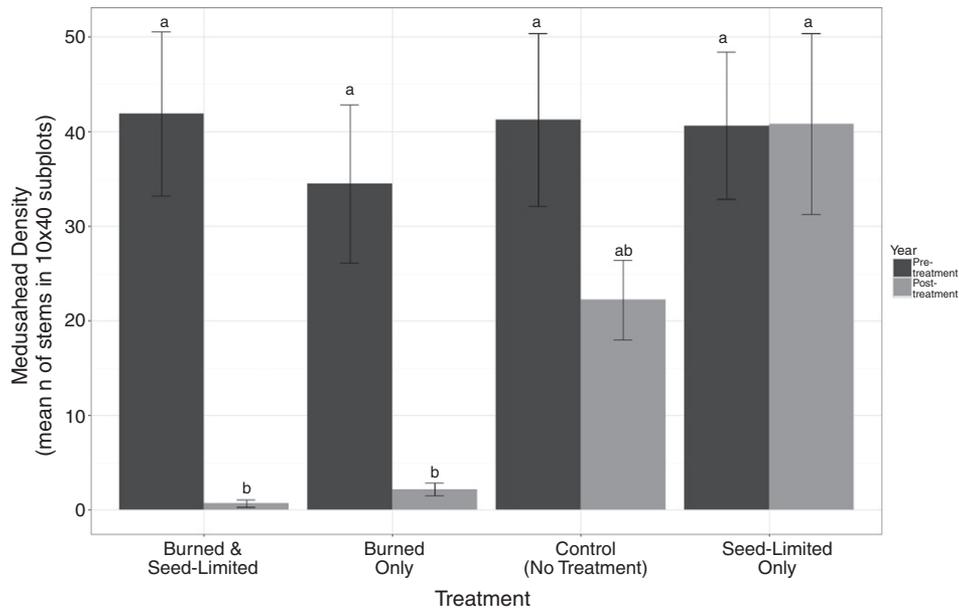
Figure 4. Treatment effects on mean medusahead densities from 10 × 40 cm subplots. Burning was significant different from the control group in all cases, but the effect size increased with medusahead pretreatment dominance and further again with seed limitation. Seed limitation where medusahead dominated increased its own stemcount.

states of plots before and after treatment showed that all plots went through one of five possible shifts or showed no change (Table 2).

Discussion

Treatment Effects on Seeds and Focal Species Densities

The germination rates of burned medusahead seeds compared with unburned medusahead seeds and burned seeds of other species indicate a fundamental level of burn success, as the objective of the burn was to specifically negatively impact medusahead populations while having a less limiting effect on other more desirable species. However, burning alone was not as successful a treatment as when combined with seed-dispersal limitation. While fire successfully killed seeds (Sweet et al.,

2008), dispersal in from plot edges will eventually limit treatment effectiveness. This is further shown in our seed-rain measurements, where accumulations were highest in burned plots that were not seed limited.

While treatments had a strong limiting effect on medusahead population densities, they had no notable effect on population densities of wild oat or needlegrass in the first year after treatment. An important area for future research would be to study potential effects of these treatments on all three focal species at this scale in proceeding years, as this study was limited to first year after treatment, and delayed effects on population dynamics are possible. For instance, the increased wild oat fecundity observed in the first year after treatment may correlate with an increase in wild oat densities 2 yr after treatment. Both this and the longevity of such a population boost should be investigated. The lack of treatment effect on needlegrass densities in the first year after
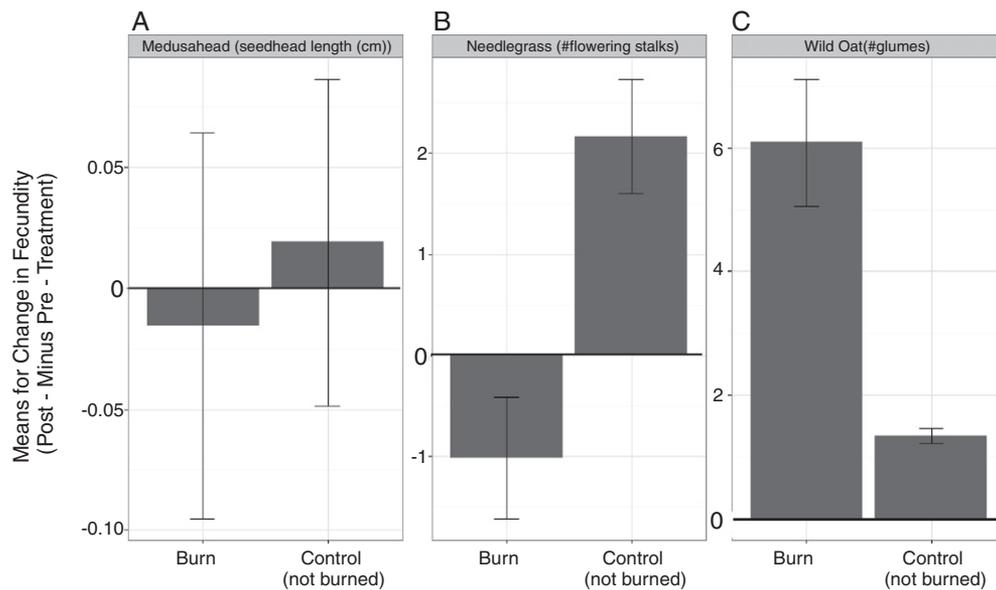
Figure 5. Changes in mean fecundity by dominant species. **A,** Treatment had no significant effect on medusahead fecundity (mean seed-head lengths from 10 × 40 cm subplot). **B,** Burning reduced needlegrass fecundity (mean number of flowering stalks per bunch per 1-m plot) while unburned needlegrass saw increased fecundity that year. **C,** Burning significantly increased oat fecundity (mean number of glumes per individual from 10 × 40-cm subplot) with a statistically significant difference from not burning.

Table 1
Breakdown of clustering for plot vegetation types generated through cluster analysis. Each cluster consists of one or more indicator species that identify that state.

Cluster	Indicator species	Scientific name	Mean abundance	Standard deviation of sample mean	P value
1	Medusahead	*Elymus caput-medusae*	27.6	1.42	0.0002
2	Wild oat	*Avena spp. (barbata & fatua)*	21.8	3.26	0.0002
3	Broadleaf filaree	*Erodium botrys*	27.4	1.43	0.0002
3	Redstem filaree	*Erodium cicutarium*	15.5	3.56	0.0004
4	Foxtail brome	*Bromus madritensis*	10.5	3.28	0.0002
4	Purple needlegrass	*Stipa pulchra*	22.2	2.98	0.0002
4	Wall bedstraw	*Galium parisiense*	6.8	3	0.0004
4	Prickly lettuce	*Lactuca serriola*	18.8	3.24	0.0018
4	Purple false brome	*Brachypodium distachyon*	5.1	2.66	0.0064
4	Blue fieldmadder	*Sherardia arvensis*	3.9	2.31	0.0078
4	Garden vetch	*Vicia sativa*	7.2	3.05	0.009

treatment indicates that using prescribed fire where needlegrass and medusahead coexist for restoration could be a responsible treatment option, as the impact on needlegrass is similar with or without treatment, yet treatment strongly negatively impacts medusahead. In addition, other studies have previously shown that prescribed fire can have a delayed positive impact on needlegrass population dynamics (Dyer, 2003), which would create a beneficial inverse effect of treatments improving needlegrass populations while limiting medusahead populations.

Specific effects of treatments on medusahead population densities showed that burning had a significant negative effect. Dispersal limitation further increased burn effects by reducing seed input from surrounding areas. Where plots were burned but not seed limited, the highest seed-rain inputs were seen, counteracting some of the beneficial effects of the fire by creating openings for new invasion.

Needlegrass, wild oat, and medusahead in control plots showed reduced stemcounts in year two. These data and weather data suggest that year two of the experiment was likely a low productivity year in general for grasses on the basis of drought. The abiotically driven tendencies of annual rangeland in California further support this contention (Bartolome et al., 2007). However, seed-rain data in medusahead − dominated plots indicate that medusahead stemcount reduction is a result of more than just annual weather variation. Medusahead seed rain in untreated medusahead − dominated plots was significantly lower than in burned plots where space had been cleared due to fire. This is a result of a dense medusahead thatch layer, which seems to prevent seeds from reaching the soil surface and similarly prevents seeds from establishing, according to seed rain trap data.

In medusahead − dominated plots, the seed-limitation treatment—reducing propagule pressure from the plot buffer area—without the combined effect of fire, resulted in an increased stemcount. Through increased availability of resources such as light and water, more seeding stems were produced and survived through the thatch. More research is needed to determine whether these came from an increase in the number of germinated seeds or an increase in the number of flowering stems per seed. Burning and seed limiting resulted in the biggest reduction in medusahead stemcount, due to removal of medusahead seed from edges. This highlights the importance of considering edge effects when planning treatment units.

The spread of seed-rain count data was narrow in plots that were not burned but much wider in burned plots. This may be explained by medusahead's thatching tendencies. Medusahead litter decomposes more slowly than most other species due to its high silica content (Bovey et al., 1961). On the basis of seed-rain counts, it seems that medusahead's tendency to form dense mats of undecomposed litter might result in fewer seeds arriving at the soil surface. Seed-rain data under untreated thatch combined with observed reduced stemcounts in untreated patches suggest that medusahead becomes self-limiting once it reaches dense populations, but more research is needed to determine this distinctly from the possibility that observed trends were merely due to plant plasticity in fecundity or stemcount.

Table 2
Transitions between vegetation types pretreatment to post-treatment, sorted by treatment type. Number of plots with a common treatment and transition is shown, as well as mean species richness for those plots pretreatment (year one).

Transition (year one → year two)	Treatment	No. plots	Mean richness, year one	Standard deviation richness, year one
Medusahead → Needlegrass mix	Control	2	9.0	0.0
Medusahead → Needlegrass mix	Seed-limited/not burned	2	9.0	0.0
Medusahead → Filaree	Burned & limited	5	8.0	1.3
Medusahead → Filaree	Burned/not limited	7	8.7	1.5
Medusahead → Filaree	Control	1	7.0	0.0
Medusahead → Filaree	Seed-limited/not burned	1	9.0	0.0
Needlegrass mix → Filaree	Burned & limited	2	10.5	0.5
Needlegrass mix → Filaree	Burned/not limited	1	13.0	0.0
Needlegrass mix → Needlegrass mix	Burned & limited	2	10.0	3.0
Filaree → Filaree	Burned & limited	1	7.0	0.0
Wild oat → Wild oat	Burned & limited	4	8.0	1.2
Needlegrass mix → Needlegrass mix	Burned/not limited	2	11.0	2.0
Wild oat → Wild oat	Burned/not limited	4	8.5	0.9
Medusahead → Medusahead	Control	7	8.0	2.3
Wild oat → Wild oat	Control	2	8.0	1.0
Medusahead → Medusahead	Seed-limited/not burned	5	8.4	1.5
Needlegrass mix → Needlegrass mix	Seed-limited/not burned	1	11.0	0.0
Filaree → Filaree	Seed-limited/not burned	1	8.0	0.0
Wild oat → Wild oat	Seed-limited/not burned	2	8.0	1.0
Filaree → Medusahead	Control	2	8.0	1.0
Filaree → Medusahead	Seed-limited/not burned	1	11.0	0.0
Filaree → Wild oat	Burned & limited	1	11.0	0.0
Filaree → Wild oat	Burned/not limited	1	11.0	0.0
Filaree → Wild oat	Control	1	8.0	0.0
Filaree → Wild oat	Seed-limited/not burned	2	6.5	0.5

Burning reduced medusahead populations beyond the reduction seen in controls in all treatment groups, but to different extents. Adding one extra meter of seed-limitation surrounding the plot strongly reduced the availability of seeds to the treated area, indicating that treatments will be most effective where they exceed medusahead's relatively short dispersal distances to limit invasion from treatment edges (likely only slightly larger than 9 m^2, the size of the seed-limited & burned areas in this study). However, this effective 1-m buffer used in our study comes from a site where cattle grazing was excluded. This dispersal distance changes with cattle grazing, where seeds have been found to travel up to 160-m on cattle (Chuong et al., 2016). Effective prevention of reinvasion will depend on the available seedstock outside a planned treatment area and on grazing presence and pressure (Monaco et al., 2005; Davies and Sheley, 2007; Davies, 2008).

Fecundity Responses to Treatments

The null hypothesis was that the fecundities of focal species would not be changed significantly by fire treatment. Previous research on other annual grass species has shown varying levels of plasticity for fecundity in response to environmental conditions (Volis, 2009). Our results suggest the null hypothesis only held true for medusahead fecundity. Wild oat fecundity responded very positively to fire with a highly significant correlation to treatment, likely due to nutrient release. Needlegrass showed slight fecundity reduction where it was burned. Previous anecdotal studies show this fecundity reduction to be expected, but it is limited to 1 or 2 yr after the burn and is followed by a surge of needlegrass germination (Menke, 1992), but more thorough research investigation is needed to confirm this.

Plot Vegetation Types, Shifts, and Important Drivers

Four clusters, or vegetation types, became apparent for plots in each year one and year two in the analysis of the percent cover data. The life history traits of needlegrass (Bartolome and Gemmill, 1981) result in open space around bunches to be inhabited by other species and a diverse array of indicator species found in this community. These plots transitioned to a filaree type when burned due to filaree's typical strong response to fire (DiTomaso et al., 2005) and removal of thatch. In these plots, filaree is not replacing needlegrass, but the low-stature rosettes approach 100% cover. According to Menke (1992), this could be of concern in future years as this dense understory can negatively impact germination of needlegrass. Filaree plots also had high medusahead or wild oat presence, so many of these moved to medusahead— or wild oat—dominated states if left untreated. This is expected as filaree is a disturbance-adapted plant, showing significant increases in germination where openings are created by activity (Schiffman, 2011). Therefore, where there is a lack of disturbance, other species are likely to become more dominant over time. Wild oats' increased fecundity after fire caused the observed shifts from filaree to wild oat dominance. The adverse effect of the fire treatment on medusahead seed germinability, combined with filaree's strong response to fire, caused the transition of all medusahead plots to filaree. This is consistent with research by George et al. (1992), which shows filaree as a competitive forb after fire in annual rangeland due to its drought tolerance and fast-growing tap root.

Implications

In early-detection and rapid-response scenarios (Brooks, 2008), managers may try a targeted approach, treating entire medusahead patches. Managers should also ensure that treatment scale is significant enough to minimize seed encroachment from treatment edges by considering what species occur in the boundaries and their invasibility. Medusahead fecundity did not respond to changes in resource availability associated with burning, while wild oats had a significant positive response. This suggests that where managers use fire on medusahead—infested pastures with a wild oat seedbank, they have the ability to promote this more desirable species as a side effect. Further research can identify what other species have strong fecundity responses to fire timed at reducing medusahead populations.

References

Bartolome, JW, Gemmill, B, 1981. The ecological status of *Stipa Pulchra* (Poaceae) in California. Madrono 28 (3), 172–184.

Bartolome, JW, Barry, WJ, Griggs, T, Hopkinson, P, 2007. Valley grassland. In: Barbour, M., Keeler-Wolf, T., Schoenherr, A. (Eds.), Terrestrial vegetation of California, third ed. University of California Press, Berkeley, CA, USA, pp. 367–393.

Blondel, J, 2003. Guilds or functional groups: does it matter? Oikos 100, 223–231.

Bovey, RW, Tourneau, DLE, Erickson, LC, 1961. The chemical composition of medusahead and downy brome. Weeds 9, 307–311.

Brooks, ML, 2008. Plant invasions and fire regimes. Wildland fire in ecosystems: effects of fire on flora. US Forest Service RMRS-GTR-42, Fort Collins, CO, USA, pp. 33–45.

Chuong, J, Huxley, J, Spotswood, EN, Nichols, L, Mariotte, P, Suding, KN, 2016. Cattle as dispersal vectors of invasive and introduced plants in a California annual grassland. Rangeland Ecology & Management 69, 52–58.

Davies, KW, 2008. Medusahead dispersal and establishment in sagebrush steppe plant communities. Rangeland Ecology & Management 61, 110–115.

Davies, KW, Sheley, RL, 2007. A conceptual framework for preventing the spatial dispersal of invasive plants. Weed Science 55, 178–185.

Davies, KW, Svejcar, TJ, 2008. Comparison of medusahead-invaded and noninvaded Wyoming Big Sagebrush Steppe in southeastern Oregon. Rangeland Ecology & Management 61 (6), 623–629.

DiTomaso, JM, Enloe, SF, Pitcairn, MJ, 2007. Exotic plant management in California annual grasslands. Ecology and Management of California Grasslands 281–296. Chapter 22.

DiTomaso, JM, Kyser, GB, Hastings, MS, 1999. Prescribed burning for control of yellow starthistle *(Centaurea solstitialis)* and enhanced native plant diversity. Weed Science 47, 233–242.

DiTomaso, JM, Kyser, GB, McDougald, NK, Vargas, RN, Doran, MP, Wilson, R, Orloff, S, 2005. Medusahead control. Proceedings of the California Weed Science Society 57, 145–148.

Duncan, CA, Jachetta, JJ, Brown, ML, Carrithers, VF, Clark, JK, DiTomaso, JM, Lym, RG, McDaniel, KC, Renz, MJ, Rice, PM, 2009. Assessing the economic, environmental, and societal losses from invasive plants on rangeland and wildlands. Weed Technology 18, 1411–1416.

Dyer, AR, 2003. Burning and grazing management in a California grassland: growth, mortality, and recruitment of *Nassella pulchra*. Restoration Ecology 11 (3), 291–296.

George, MR, Brown, JR, Clawson, WJ, 1992. Application of nonequilibrium ecology to management of Mediterranean grasslands. Journal of Range Management 436–440.

Hironaka, M, 1961. The relative rate of root development of cheatgrass and medusahead. Journal of Range Management 14, 263–267.

Kyser, GB, DiTomaso, JM, 2002. Instability in a grassland community after the control of yellow starthistle *(Centaurea solstitialis)* with prescribed burning. Weed Science 50, 648–657.

Kyser, GB, Doran, JM, McDougald, NK, Orlaff, SB, Vargas, RN, Wilson, RG, DiTomaso, JM, 2008. Site characteristics determine the success of prescribed burning for medusahead *(Taeniatherum caput-medusae)* control. Invasive Plant Science and Management 1, 376–384.

Lytle, DJ, 1998. Soil survey of Yuba County, California. US Department of Agriculture, NRCS, Davis, CA, USA.

Mangla, S, Sheley, RL, James, JJ, 2011. Field growth comparisons of invasive alien annual and native perennial grasses in monocultures. Journal of Arid Environments 75, 206–210.

McCune, B, Mefford, MJ, 1999. PC-ORD. Multicariate analysis of ecological data. Version 4. MjM Software Design, Gleneden Beach, OR, USA.

Menke, JW, 1992. Grazing and fire management for native perennial grass restoration in California grasslands. Fremontia 20 (2), 22–25.

Monaco, TA, Osmond, TM, Dewey, SA, 2005. Medusahead control with fall- and spring-applied herbicides in northern Utah foothills. Weed Technology 19, 653–658.

Quinn-Davidson, LN, Varner, JM, 2011. Impediments to prescribed fire across agency, landscape and manager: an example from northern California. International Journal of Wildland Fire 21, 210–218.

Schiffman, PM, 2011. Understanding California grassland ecology. Fremontia 12.

Sweet, SB, 2005. Effect of seed maturity on the resistance of weed seeds to simulated fire: implications for prescribed burns [thesis] University of California, Davis, CA, USA (56 pp.).

Sweet, SB, Kyser, GB, DiTomaso, JM, 2008. Susceptibility of exotic annual grass seeds to fire. Invasive Plant Science and Management 1, 158–167.

Volis, S, 2009. Plasticity, its cost, and phenotypic selection under water and nutrient stress in two annual grasses. Biological Journal of the Linnean Society 97, 581–593.

Walker, B, Kinzig, A, Langridge, J, 1999. Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. Ecosystems 2 (2), 95–113.