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Burning reveals cryptic plant diversity and promotes coexistence in a California prairie restoration experiment

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Abstract. Grassland and prairie restoration projects in California often result in long-term establishment of only a few native plant species, even when they begin with a diverse seed palette. One explanation for the disappearance of certain native species over time is that they are excluded through competition. If so, management that reduces interspecific competition may favor "subordinate" natives and promote greater native species diversity in restored communities. Potential management approaches to accomplish this goal include intraspecific spatial aggregation during seeding and prescribed fire. However, no studies have experimentally evaluated the effects of fire on a controlled (restoration) species pool or the interaction between fire and spatial aggregation. In a previous California prairie restoration experiment, we demonstrated that aggregated plantings protected competitively subordinate species from exclusion and increased community diversity for three years. However, native species richness declined throughout the study, and the benefits of aggregated seeding had begun to disappear by the third year. For the present study, we resurveyed the experimental plots five years after seeding and in the following year carried out controlled burns on half of the plots. The four subordinate species and one of the previously dominant species continued to decline and essentially disappeared aboveground during years four and five. However, burning in year five decreased the cover of dominant natives, triggered the reappearance of the three subordinate species that had disappeared or nearly disappeared in previous years, and increased diversity of the restored community. Seeding treatments (aggregated or interspersed) did not significantly affect community-level responses to the burning treatment. These results confirm that although initial intraspecific aggregation may promote species coexistence in the short term, re-establishing disturbance regimes can allow coexistence over a longer time scale by revealing and potentially renewing seed bank diversity.

Key words: California; Central Valley; controlled burns; diversity; fire; fire-induced recruitment; grassland; *Grindelia*; intraspecific aggregation; restoration; seed bank; *Trifolium*.

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INTRODUCTION

Competitive exclusion of competitively inferior, or "subordinate," species can reduce species diversity in both natural and anthropogenic plant communities (Grime 1973). Some of the most striking experimental examples of this are found in restoration projects, where it is common for species-rich seed mixes to result in established communities that include only a few of the seeded species (Lulow 2004, Stromberg et al. 2007). Several experiments have demonstrated that allowing subordinate species to establish before they face competition from more dominant species—either by planting them in advance or by planting species in a spatially aggregated design—can prolong the existence of subordinates and thereby increase species diversity (Hodge et al. 1996, Stoll and Prati 2001, Corbin and D'Antonio 2004, Fukami et al. 2005, Porensky et al. 2012, Yurkonis and McKenna 2014). Most such studies are relatively short-term, however, leaving it unclear whether such diversity benefits can persist in the face of long-term competitive (successional) challenges.

We previously showed that creating intraspecific spatial aggregation during seeding could create temporal priority and increase plant species diversity for at least three years after seeding (Porensky et al. 2012). However, the benefits of spatially-aggregated seeding began to decline in the third year, largely due to a decrease in the cover of subordinate species. The decline of subordinates over time implies that aggregated seeding (conferring spatial priority) might only delay competitive exclusion of subordinate species by dominant competitors but not prevent it in the long term. Additional management may thus be necessary to maintain long-term diversity.

In many systems, competitively inferior species depend on disturbance in order to persist in the presence of superior competitors (Dirzo et al. 1992, Guo 2001, Porensky et al. 2013). Such species take advantage of resources made available by disturbance, but they may decline again as competitively superior species become reestablished (Tilman 1985, Grime 1988). In disturbance-prone systems, temporary lack of disturbance can thus lead to apparent decreases in diversity. However, competitively inferior species commonly persist in the seed bank (Keeley 2006), and by releasing such species, disturbances can reveal otherwise cryptic diversity.

Fire has been an important disturbance in many California ecosystems, including grasslands and prairies, for at least the last 10,000 years (Wills 2006, Bartolome et al. 2007, Reiner 2007). Fire-prone systems can have rich seed banks of ephemeral plant species that may only appear aboveground in rare post-fire years and then become replaced by community dominants (Keeley 2006). In fire-adapted systems, it is common for species richness to increase following fire—apparently due to reduction in competitive exclusion of subordinate species by dominants (Copeland et al. 2002)—but then to decline with increasing time after fire (Engle et al. 2000, Keeley 2006). In addition, chemicals in smoke and other fire-related cues can break dormancy in a wide range of plant species, even in unburned areas adjacent to burns (Keeley 1987, Baxter et al. 1994, Keeley and Fotheringham 1997, Read and Bellairs 1999, Flematti 2004, Ghebrehiwot et al. 2013, Reynolds et al. 2014).

Fire can favor the ephemeral forb component, in particular, of grassland and prairie communities, with native annual forbs increasing in abundance and/or species richness and sometimes dominating sites the year after fire (Hervey 1949, Antos et al. 1983, DiTomaso et al. 1999, Meyer and Schiffman 1999, Copeland et al. 2002, Howe 2011). Some of the increased annual forb abundance may be linked to reduced competition from perennial grasses following a burn (Engle et al. 2000, Seabloom et al. 2005).

While disturbance tends to release ephemeral species and thus increase species richness and diversity, it is less clear how disturbance interacts with spatial structure in vegetation and how this interaction affects native species diversity and coexistence. In some systems, fire can strengthen patchy vegetation distributions and thereby maintain community diversity across a landscape (Watt 1947, Morrison et al. 1995, Fuhlendorf and Engle 2004, Schoennagel et al. 2008); in other systems, fire can have a homogenizing effect (Seabloom et al. 2005). Despite the uncertainty regarding the spatial effects of fire on diversity, few studies have examined how the effects of fire in structuring grassland or prairie communities depend on pre-fire spatial community structure and successional trajectories.

We explored whether fire could reverse the decline in native species diversity in our spatial priority experiment (Porensky et al. 2012) and whether this positive effect of fire is stronger when species are seeded in intraspecific clusters rather than interspersed. We tested these questions using a replicated series of controlled burns

Table 1. Selected traits of seeded species.

Species	Life history and life form	Stature	Dispersal mode	Dominance classification†
Calandrinia ciliata (Ruiz & Pav.) DC	annual forb	low	gravity	subordinate
Elymus glaucus Buckl.	perennial bunchgrass	tall	gravity	dominant
Elymus trachycaulus (Link) Shinners	perennial bunchgrass	tall	gravity	dominant
Elymus triticoides Buckley	perennial rhizomatous grass	tall	gravity	dominant
Grindelia camporum Greene	perennial forb	tall	wind	dominant
Melica californica Scribn.	perennial bunchgrass	medium	gravity	subordinate
Stipa pulchra Hitchc.	perennial bunchgrass	medium	gravity	dominant
Trifolium bifidum A. Gray	annual forb	low	gravity	subordinate
Trifolium willdenovii Spreng.	annual forb	low	gravity	subordinate

† As classified by Porensky et al. (2012; see *Methods*).

in our previously-seeded experiment. We predicted that fire would increase the abundance of subordinate species, and especially so when species were seeded in intraspecific clusters, thus highlighting disturbance as a mechanism for maintaining species diversity in a restoration setting.

METHODS

Study site

The experimental plots are located in the Plant Sciences Agricultural Research Fields on the University of California, Davis campus (38.54° N, 121.78° W). Soil at the study site is classified as Yolo Silt Loam and the site was maintained fallow by biannual tilling for at least three years prior to the start of this experiment. The site is located in the Central Valley of California and experiences an interior Mediterranean climate with a high inter- and intra-annual variability in both the amount and timing of precipitation. Summer (dry season) maximum temperatures average 32°C, and winter (wet season) minimum temperatures average 5°C. Over the past 55 years, annual mean precipitation at a station <5 km from the study site has been 442 mm (range: 152–914 mm), with more than 95% of the total annual precipitation falling between October and April. During the first water year of our study (August 2007–July 2008), total precipitation was 9% below average. During Year 2, precipitation was 10% below average. During Years 3 and 4, precipitation was 16% and 32% above average, respectively. In Years 5 and 6, precipitation was 26% and 14% below average, respectively. The historical fire regime of California Central Valley native vegetation is not known, but evidence suggests Native Americans frequently conducted burns within the region (Wills 2006, Bartolome et al. 2007, Reiner 2007). Our study site has been in agricultural use and has not been subject to burning for at least 100 years.

Experimental design

We established 19 octagonal plots in 2008. Each plot has a diameter of 5 m, and plots are separated from one another by 2 m. We planted each plot with eight native California prairie species on 6–8 February 2008, irrigated them once at the end of March 2008, and periodically weeded them until July 2009. After we discontinued weeding, the plots were invaded by non-native species.

The seeded species consisted of four perennial grasses (*Elymus glaucus*, *Elymus triticoides*, *Melica californica* and *Stipa* (*Nassella*) *pulchra*), two non-leguminous forbs (annual *Calandrinia ciliata* and perennial *Grindelia camporum*), and two annual leguminous forbs (*Trifolium bifidum* and *Trifolium willdenovii*) (Table 1). During the first growing season we discovered that our *E. glaucus* seed also included seed of the native grasses *E. triticoides* and *E. trachycaulus*. Therefore, we summed cover of all *Elymus* species at the plot level for statistical analyses.

Based on observed competitive dynamics during the first three years of the experiment, Porensky et al. (2012) classified each seeded species as either "aggressive" (dominant) or "subordinate". The species classified as dominant were those that exhibited greater increases in cover in interspersed than in aggregated plots. Porensky et al. (2012) classified *Elymus* spp., *G. camporum*, and *S. pulchra* as dominant and the remaining seeded species as subordinate. Selected

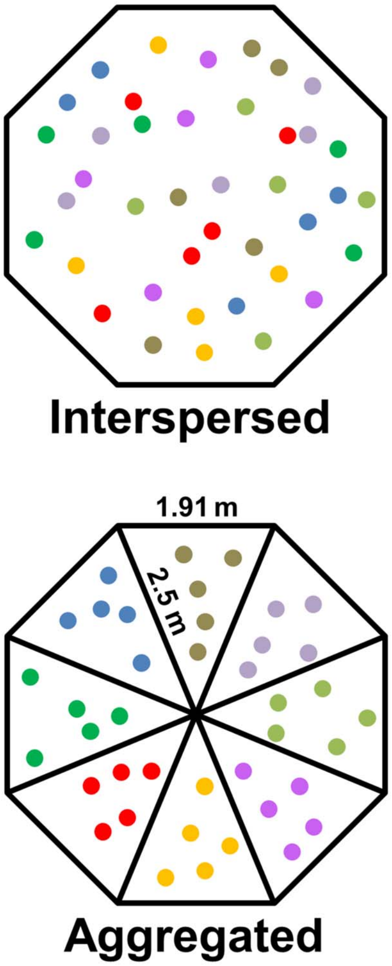

Fig. 1. Planting designs for interspersed and aggregated plots. Each color represents seed of one species.

traits of the seeded species are listed in Table 1.

We assigned six randomly selected plots to the 'interspersed' treatment and broadcast-seeded them with the eight-species mixture. In the 13 remaining plots, we broadcast-seeded each of the eight species into a wedge-shaped 2.2 m^2 sector of each octagonal plot to create an 'aggregated' arrangement (Fig. 1). All plots received the same mass of seed per species.

On 19 October 2012, the UC Davis Fire Department performed 10 controlled burns on 7 aggregated and 3 interspersed plots, randomly selected within these treatment classes from the original 19 hexagonal plots. The burns were carried out from 1 to 3 pm and resulted in the combustion of nearly all aboveground plant biomass (flame heights 3–5 m). During burning, the maximum air temperature was 27°C, relative humidity was 34%, and winds were from the south at 11 km/h.

Annually between 2008 and 2013, we quantified the percent cover of each seeded species (with the exception of *G. camporum*, *S. pulchra*, and *Elymus* spp. in 2011) at the peak of flowering (April–July, depending on the species and year). For each species, we visually estimated percent cover within each wedge and then averaged cover at the plot level prior to analysis.

Statistical analyses

For each plot, we calculated diversity of our seeded species from cover data using the Shannon-Wiener Index (Shannon 1948), which incorporates species richness and evenness. We used generalized linear models (GLMs) to analyze Year 6 Shannon-Weiner index, species richness, and total percent cover of seeded species–as well as percent cover by species–as response variables, with aggregation treatment, burn treatment, and their interaction as predictor variables. We also used a GLM to analyze Shannon-Weiner index in Year 5, before plots were burned, using aggregation treatment as the only predictor. Depending on response variable and species, we modeled the response distribution as normal, log-normal, or binomial (Table 2) to meet model assumptions. We performed all analyses at the plot level using the function 'glm' in R 3.1.0 (R Development Core Team 2014).

RESULTS

For results from Years 1–3, see Porensky et al. (2012). Richness and Shannon-Weiner diversity of seeded species continued to decrease through Year 5 (Fig. 2). This decrease was partially driven by a continued decline of *Calandrinia ciliata*, *Trifolium bifidum*, and *Trifolium willdenovii*, three of the four species classified as subordinate by Porensky et al. (2012), to zero or near-zero cover by Year 5 after seeding, even in the aggregated plots where they had initially resisted encroachment by more dominant species (Fig. 3). In addition, *Grindelia camporum*, a species identified as dominant by Porensky et al. (2012), began to decline dramatically in cover after Year 3 (Fig. 3).

Table 2. Effect of aggregation (Agg) and burning (Burn) on percent cover and diversity.

Response	Dist/transf	Effect	Coefficient	SE	*z* or *t*	*p*
Year 6						
Percent cover						
C. ciliata	Binomial	Burn	3.114	0.727	4.280	<**0.001**
		Agg	−0.288	0.916	−0.314	0.75
		Burn × Agg	−0.495	0.941	−0.526	0.60
T. willdenovii	Log-normal	Burn	6.188	2.011	3.077	**0.008**
		Agg	0.806	1.742	0.463	0.65
		Burn × Agg	−2.680	2.434	−1.101	0.29
T. bifidum	Log-normal	Burn	5.802	1.193	4.863	<**0.001**
		Agg	0.000	1.033	0.000	1.00
		Burn × Agg	−2.583	1.444	−1.789	0.09
S. pulchra	Binomial	Burn	−1.451	0.219	−6.635	<**0.001**
		Agg	−1.201	0.161	−7.480	<**0.001**
		Burn × Agg	0.923	0.288	3.209	**0.001**
M. californica	Binomial	Burn	−0.406	0.917	−0.442	0.66
		Agg	0.000	0.711	0.000	1.00
		Burn × Agg	0.657	1.059	0.620	0.54
G. camporum	Log-normal	Burn	2.829	0.737	3.841	**0.002**
		Agg	1.108	0.638	1.737	0.10
		Burn × Agg	−2.418	0.891	−2.713	**0.016**
Elymus spp.	Binomial	Burn	−1.964	0.386	−5.083	<**0.001**
		Agg	0.184	0.173	1.064	0.29
		Burn × Agg	1.246	0.415	3.001	**0.003**
Total	Normal	Burn	−32.208	13.77	−2.339	**0.034**
		Agg	−25.865	11.925	−2.169	**0.047**
		Burn × Agg	23.421	16.662	1.406	0.18
Species richness	Normal	Burn	2.000	0.496	4.036	**0.001**
		Agg	0.000	0.429	0.000	1.00
		Burn × Agg	−0.524	0.600	−0.874	0.40
Shannon-Weiner index	Normal	Burn	0.561	0.180	3.123	**0.007**
		Agg	0.164	0.156	1.057	0.31
		Burn × Agg	−0.061	0.217	−0.283	0.78
Year 5						
Shannon-Weiner index	Normal	Agg	0.338	0.081	4.167	<**0.001**

Notes: "Dist/transf" indicates the distribution and/or transformation used to model the response of cover, richness, or diversity of seeded species to burning and aggregation. For binomial models, we report the z value; for normal and log-normal models, we report the t value. For all Year 6 responses, we present models fit with using aggregation, burning, and their interaction as predictors; for Year 5 Shannon-Weiner index, we present a model using aggregation as the only predictor, as plots had not yet been burned. All models have 15 degrees of freedom, except the model for Year 5 Shannon-Weiner index, which has 17. The p values <0.05 appear in boldface.

Despite the disappearance of *T. bifidum* and *T. willdenovii* and near-disappearance of *C. ciliata* in both interspersed and aggregated plots by Year 5, Shannon-Wiener diversity was significantly greater in aggregated plots ($p < 0.001$; Fig. 2; Table 2). This differentiation was driven mainly by the fact that *G. camporum* and *Elymus* spp. cover declined more in interspersed than in aggregated plots (Fig. 3).

By Year 6, richness and Shannon-Weiner diversity of the seeded species did not differ significantly between the two planting arrangements (both $p > 0.30$; Fig. 2; Table 2). As in previous years, total cover of all seeded species combined was lower in aggregated plots (31.1% ± 4.3%) than in interspersed plots (45.5% ± 10.3%; $p = 0.047$; Fig. 3; Table 2). For individual species, however, the effect of planting arrangement (i.e., the difference in species-specific cover between aggregated and interspersed plots) had decreased to nonsignificant levels (all $p > 0.10$; Fig. 3; Table 2) for all species except *Stipa pulchra*, which had three times as much cover in interspersed than in aggregated plots ($p < 0.001$; Fig. 3; Table 2).

In Year 6, the three subordinate species that had declined to zero or near-zero cover (*C. ciliata, T. bifidum, and T. willdenovii*) reappeared in the burned treatments while remaining virtually absent in the unburned treatments ($p < 0.01$; Fig. 3; Table 2). The fourth subordinate species (*Melica californica*) did increase substantially in Year 6, but not more so in the burned plots ($p = 0.66$; Fig. 3; Table 2). No subordinate species showed a significantly different response to burning in aggregated vs. interspersed plots (all

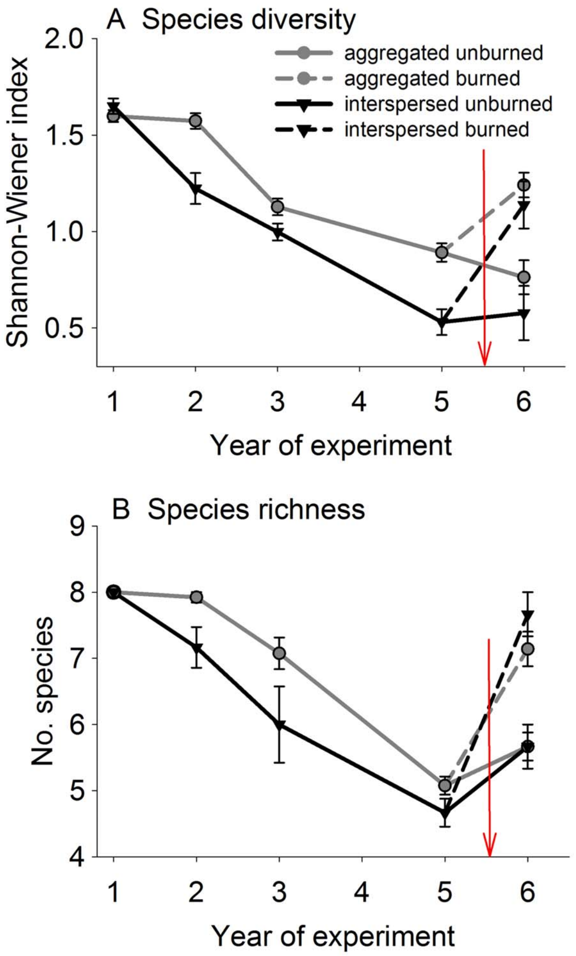

Fig. 2. Species richness and Shannon-Weiner diversity of seeded species during the six years of the study. Gray lines represent aggregated seeding, dark lines represent interspersed seeding, dashed lines represent burned plots, and solid lines represent unburned plots. Before 2013, vertices represent values of aggregated and interspersed plots regardless of ultimate burning treatment applied. Error bars represent one standard error. The vertical arrow indicates the date on which plots were burned.

$p > 0.09$; Fig. 3; Table 2).

Among the dominant species, *S. pulchra* and *Elymus* spp. remained abundant in all treatments through Year 6 (Fig. 3). Burning reduced *S. pulchra* cover by 65% and *Elymus* spp. cover by 63% (both $p < 0.001$; Fig. 3; Table 2), and more so in interspersed plots (both $p < 0.003$; Fig. 3; Table 2). In contrast, burning increased the cover of *G. camporum*, which had virtually disappeared from the plots ($p = 0.002$), particularly in the interspersed plots (burn × aggregation interaction: $p = 0.016$; Fig. 3; Table 2). However, even in the interspersed, burned plots, mean *G. camporum* cover only reached 2.0%.

Burning substantially increased Shannon-Weiner diversity of seeded species ($p = 0.007$; Fig. 2, Table 2), restoring it to a level similar to that in Year 2 or 3. Burning also increased richness of focal species by 35% ($p = 0.001$; Fig. 2; Table 2) and reduced total cover of all focal species by 37% ($p = 0.034$; Fig. 3; Table 2). However, the effect of burning on diversity, richness, and total cover of focal species was not significantly different in aggregated vs. interspersed plots (all $p > 0.18$; Figs. 2 and 3; Table 2).

DISCUSSION

Successional patterns prior to burning

The decline in richness and Shannon-Weiner diversity of seeded species in all plots through Year 5 (Fig. 2) was due to the fact that all species identified as subordinate by Porensky et al. (2012) declined to zero or near-zero cover regardless of seeding arrangement (aggregated or interspersed; Fig. 3). This decline muted the positive effect of aggregated seeding on Shannon-Weiner diversity by Year 3, but the aggregation effect reappeared again strongly in Year 5 (Fig. 2), driven mainly by *G. camporum* and *Elymus* spp., which maintained higher cover in aggregated than interspersed plots (Fig. 3).

Grindelia camporum was initially considered a dominant species by Porensky et al. (2012) based on its high cover during the first three years of the experiment and apparent suppression of other species, but it appears that its dominance decreases as succession proceeds. Our results suggest that *G. camporum* behaves more like a subordinate or mid-successional species that depends on disturbance for persistence, consistent with other studies that have documented a disappearance of *G. camporum* from restoration plantings after several years despite initial strong performance (Young et al. 2009; K. J. Vaughn, *personal communication*).

Effect of burning on native species cover and diversity

Burning significantly increased the cover of *C.*

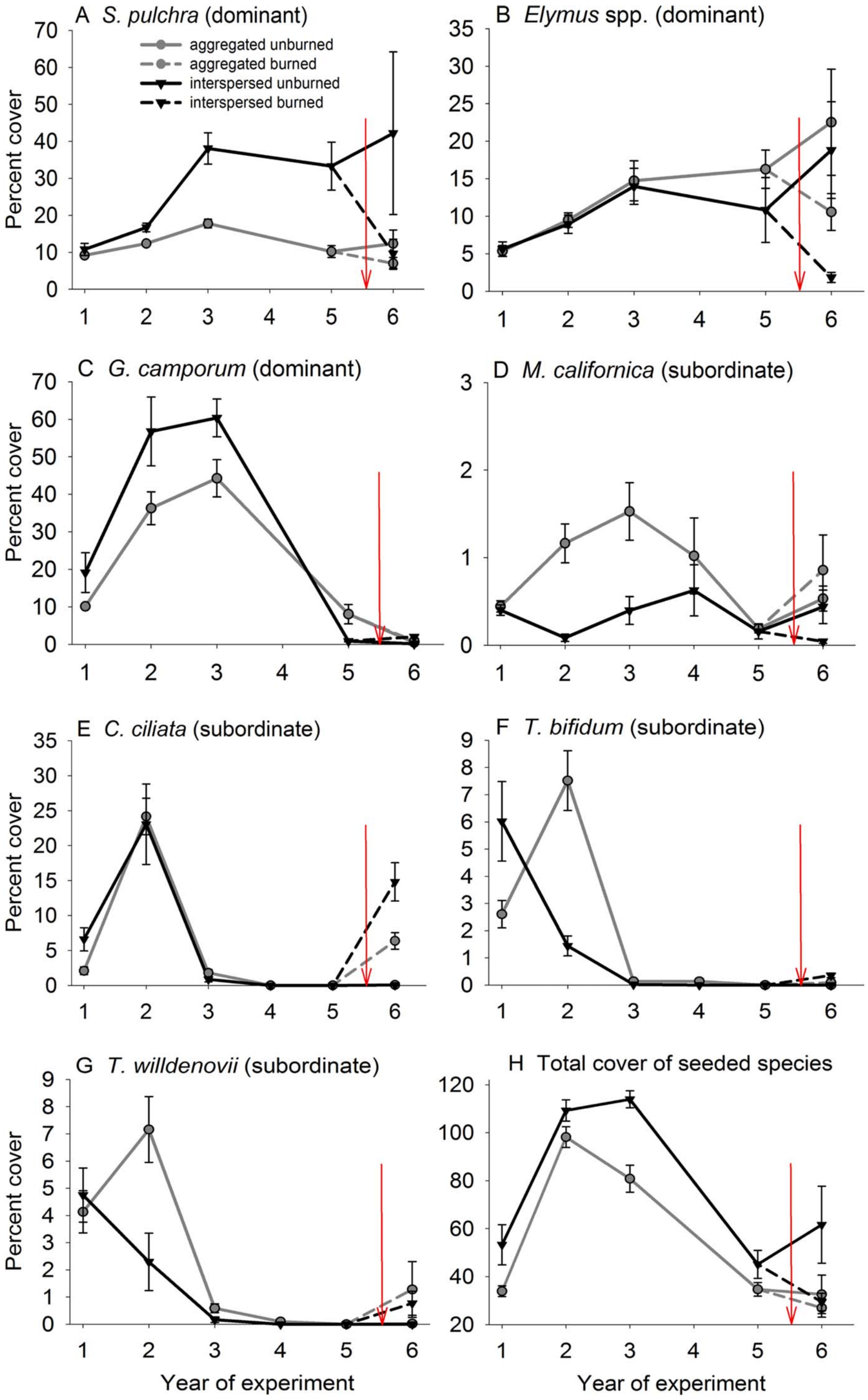

Fig. 3. Species-specific percent cover and total percent cover of seeded species during the six years of the study. Gray lines represent aggregated seeding, dark lines represent interspersed seeding, dashed lines represent burned plots, and solid lines represent unburned plots. Before 2013, vertices represent means for aggregated and interspersed plots regardless of ultimate burning treatment applied. Error bars represent one standard error. The vertical arrow indicates the date on which plots were burned.

ciliata, *T. willdenovii*, *T. bifidum*, and *G. camporum*, all of which had declined to very low or zero cover before burning (Fig. 3). The first three species were identified as subordinates (inferior competitors) by Porensky et al. (2012), and their reappearance in burned plots may reflect a reduction in competitive pressure (Tilman 1985, Grime 1988) and/or effects of heat, smoke, or other fire-related chemical cues enhancing germination (Keeley and Fotheringham 1997, Ghebrehiwot et al. 2013, Reynolds et al. 2014). Our results corroborate previous suggestions that the use of fire in grasslands can at least temporarily increase the abundance of "ephemeral" and/or competitively subordinate species and allow them to replenish their seed banks (Hervey 1949, Antos et al. 1983, DiTomaso et al. 1999, Meyer and Schiffman 1999, Copeland et al. 2002, Howe 2011). Burning produced a significant but small reappearance of *G. camporum* (to 2% cover), suggesting poor recruitment from its seed bank, even after its early dominance.

In contrast to the subordinate species, the dominant grasses *S. pulchra* and *Elymus* spp. showed significant reductions in cover due to burning. Some experimental studies have also shown a reduction in dominant native grass species after burning (e.g., Engle et al. 2000), while others have not (e.g., DiTomaso et al. 1999, Dyer 2003). Our observation that disturbance hindered dominant perennial grass species and favored subordinate annual forbs is consistent with results from studies of the effects of grazing, another form of disturbance (Hayes and Holl 2003, Porensky et al. 2013).

In our experiment, the decline in cover of dominant species, combined with the reappearance of several subordinate species, resulted in a substantial increase in richness and Shannon-Weiner diversity of our focal species in burned relative to unburned plots (Fig. 2). Our observations of fire-induced increases in diversity and richness are consistent with patterns in many fire-adapted ecosystems (Antos et al. 1983, Copeland et al. 2002, Howe 2011), including those in California grasslands (Hervey 1949, DiTomaso et al. 1999, Meyer and Schiffman 1999).

Influence of burning on the effect of aggregated seeding

The effect of intraspecific aggregation in promoting coexistence of subordinate and dominant native species—demonstrated previously by Porensky et al. (2012)—became non-significant by Year 5, suggesting that although creating temporal priority can postpone the competitive aboveground exclusion of subordinates by dominants, it cannot prevent it. Burning the plots did increase the cover of subordinates, but its effect was not stronger in aggregated treatments (no significant burn × aggregation interaction for subordinate species; Table 2, Fig. 3). We also note that by subdividing the experiment with the burning treatments, we cut our sample sizes by half, and reduced our power to demonstrate treatment differences.

The most dominant seeded species (*S. pulchra* and *Elymus* spp.), on the other hand, showed substantially greater reductions in cover due to burning in interspersed plots than in aggregated plots, in both absolute and proportional terms (Fig. 3). This observation is the opposite of the pattern we expected (i.e., that burning would restore the effect of aggregation in suppressing dominant species). The observation may indicate that these dominant native grasses had not established as completely or effectively in the interspersed vs. aggregated plantings, perhaps because they were seeded at higher local density in aggregated plots (i.e., in a single sector) than in interspersed plots (i.e., throughout the entire plot). Nonetheless, individual species-level responses were too small and/or asynchronous to detect at the community level; we observed no significant effect of burn × aggregation interaction in explaining richness and diversity of the seeded species. Thus, although fire may have 'reset' the successional state of our restoration plantings in ways that favor subordinate species, it did not appear to restore the diversity benefit of aggregated seeding, at least in the first year following burning.

A potential explanation for our observation that post-burn diversity was similar in aggregated and interspersed plots (Fig. 2) is that our data only represent *apparent* (aboveground) diversity; additional community diversity may exist in the seed bank and may be revealed by fire. Although we did not quantify seed banks in our experiment, it is possible that overall (aboveground plus seed bank) diversity remained similar across aggregated and interspersed plots throughout the entire study but that aboveground diversity was converted into "cryptic" seed bank diversity sooner following seeding in interspersed plots. Burning may have allowed seed bank diversity to appear aboveground once again, thus leading aggregated and interspersed plots to have similar aboveground diversity following burning. Similar cryptic diversity of annual species appears to underpin some desert plant communities, in which rain stimulates a transition from seed bank to aboveground diversity (Pake and Venable 1996). Despite the fact that overall diversity may remain similar in aggregated and interspersed plots over time, transitions between aboveground and seed bank diversity are important from an ecosystem function perspective; aggregated plots maintained aboveground cover of forbs (which support pollination services), including nitrogen-fixing *Trifolium* species, for more years following seeding than did interspersed plots.

Implications for restoration burns

Fire has been used as a restoration strategy in California prairies, but mainly as a weed-control measure before planting natives (Corbin et al. 2004, Moyes et al. 2005, Stromberg et al. 2007). Post-restoration fire has generally been avoided for fear that losses of restored species will exceed any release of suppressed subordinate species (Swiecki and Bernhardt 1998, Veblen et al. 2007). Our results corroborate previous findings that well-established native plants can readily withstand controlled burns (Veblen et al. 2007, Holmes et al. 2011). In fact, our results suggest that burns in restoration settings can, as in more natural settings, even increase aboveground native diversity.

CONCLUSION

This study demonstrated that burning, by reducing cover of competitively superior native species and increasing cover of subordinates, can promote co-existence among natives and thus increase native diversity. The study also highlights the strongly disturbance-dependent nature of several native species, which decline to zero or near-zero cover after several years without disturbance. However, the disturbance-dependent species are not lost from the system entirely but are rather converted into 'cryptic' (seed bank) diversity that is revealed by fire. We also showed that while aggregated seeding can prolong coexistence of dominants and subordinates, it cannot prevent competitive exclusion of subordinates indefinitely, and burning does not restore the benefits of aggregation. Nonetheless, burning appears to be a useful tool for promoting persistence of subordinate species and thus maximizing native species diversity in restored California grasslands and prairies.

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LITERATURE CITED

Antos, J. A., B. McCune, and C. Bara. 1983. The effect of fire on an ungrazed western Montana grassland. American Midland Naturalist 110:354–364.

Bartolome, J. W., W. J. Barry, T. Griggs, and P. Hopkinson. 2007. Valley grassland. Pages 367–393 *in* M. G. Barbour, Keeler-Wolf, T. and Schoenherr, editors. Terrestrial vegetation of California. University of California Press, Berkeley, California, USA.

Baxter, B. J. M., J. Van Staden, J. E. Granger, and N. A. C. Brown. 1994. Plant-derived smoke and smoke extracts stimulate seed germination of the fire-climax grass *Themeda triandra*. Environmental and Experimental Botany 34:217–223.

Copeland, T. E., W. Sluis, and H. F. Howe. 2002. Fire season and dominance in an Illinois tallgrass prairie restoration. Restoration Ecology 10:315–323.

Corbin, J. D., and C. M. D'Antonio. 2004. Competition between native perennial and exotic annual grasses: implications for an historical invasion. Ecology 85:1273–1283.

Corbin, J. D., C. D'Antonio, and S. J. Bainbridge. 2004. Tipping the balance in the restoration of native plants. Pages 154–179 *in* M. S. Gordon and S. M. Bartol, editors. Experimental approaches in conservation biology. University of California Press, Berkeley, California, USA.

Dirzo, R., C. C. Horvitz, H. Quevedo, and M. A. Lopez. 1992. The effects of gap size and age on the understorey herb community of a tropical Mexican rain forest. Journal of Ecology 80:809–822.

DiTomaso, J. M., G. B. Kyser, and M. S. Hastings. 1999. Prescribed burning for control of yellow starthistle (*Centaurea solstitialis*) and enhanced native plant diversity. Weed Science 47:233–242.

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

Engle, D. M., M. W. Palmer, J. S. Crockett, R. L. Mitchell, and R. Stevens. 2000. Influence of late season fire on early successional vegetation of an Oklahoma prairie. Journal of Vegetation Science 11:135–144.

Flematti, G. R. 2004. A compound from smoke that promotes seed germination. Science 305:977–977.

Fuhlendorf, S. D., and D. M. Engle. 2004. Application of the fire–grazing interaction to restore a shifting mosaic on tallgrass prairie. Journal of Applied Ecology 41:604–614.

Fukami, T., T. M. Bezemer, S. R. Mortimer, and W. H. van der Putten. 2005. Species divergence and trait convergence in experimental plant community assembly. Ecology Letters 8:1283–1290.

Ghebrehiwot, H. M., M. G. Kulkarni, G. Szalai, V. Soós, E. Balázs, and J. Van Staden. 2013. Karrikinolide residues in grassland soils following fire: implications on germination activity. South African Journal of Botany 88:419–424.

Grime, J. P. 1973. Competitive exclusion in herbaceous vegetation. Nature 242:344–347.

Grime, J. P. 1988. The C-S-R model of primary plant strategies—origins, implications and tests. Pages 371–393 *in* L. D. Gottlieb and S. K. Jain, editors. Plant evolutionary biology. Chapman and Hall, London, UK.

Guo, Q. 2001. Early post-fire succession in California chaparral: changes in diversity, density, cover and biomass. Ecological Research 16:471–485.

Hayes, G. F., and K. D. Holl. 2003. Cattle grazing impacts on annual forbs and vegetation composition of mesic grasslands in California. Conservation Biology 17:1694–1702.

Hervey, D. F. 1949. Reaction of a California annual-plant community to fire. Journal of Range Management 2:116–121.

Hodge, S., W. Arthur, and P. Mitchell. 1996. Effects of temporal priority on interspecific interactions and community development. Oikos 76:350–358.

Holmes, K. A., K. E. Veblen, A. M. Berry, and T. P. Young. 2011. Effects of prescribed fires on young valley oak trees at a research restoration site in the Central Valley of California. Restoration Ecology 19:118–125.

Howe, H. F. 2011. Fire season and prairie forb richness in a 21-y experiment. Ecoscience 18:317–328.

Keeley, J. E. 1987. Role of fire in seed germination of woody taxa in California chaparral. Ecology 68:434–443.

Keeley, J. E. 2006. South Coast bioregion. Pages 350–390 *in* N. Sugihara, J. W. van Wagtendonk, K. E. Shaffer, J. Fites-Kaufman, and A. E. Thode, editors. Fire in California's ecosystems. University of California Press, Berkeley, California, USA.

Keeley, J. E., and C. J. Fotheringham. 1997. Trace gas emissions and smoke-induced seed germination. Science 276:1248–1250.

Lulow, M. 2004. Restoration in California's inland grasslands: The role of priority effects and management strategies in establishing native communities, and the ability of native grasses to resist invasion by non-native grasses. Dissertation. University of California, Davis, California, USA.

Meyer, M. D., and P. M. Schiffman. 1999. Fire season and mulch reduction in a California grassland: a comparison of restoration strategies. Madroño 46:25–37.

Morrison, D. A., G. J. Gary, S. M. Pengley, D. G. Ross, B. J. Mullins, C. S. Thomas, and T. S. Anderson. 1995. Effects of fire frequency on plant species composition of sandstone communities in the Sydney region: inter-fire interval and time-since-fire. Australian Journal of Ecology 20:239–247.

Moyes, A. B., M. S. Witter, and J. A. Gamon. 2005. Restoration of native perennials in a California annual grassland after prescribed spring burning and solarization. Restoration Ecology 13:659–666.

Pake, C. E., and D. L. Venable. 1996. Seed banks in desert annuals: implications for persistence and coexistence in variable environments. Ecology 77:1427–1435.

Porensky, L. M., K. J. Vaughn, and T. P. Young. 2012. Can initial intraspecific spatial aggregation increase multi-year coexistence by creating temporal priority? Ecological Applications 22:927–936.

Porensky, L. M., S. E. Wittman, C. Riginos, and T. P. Young. 2013. Herbivory and drought interact to enhance spatial patterning and diversity in a savanna understory. Oecologia 173:591–602.

R Development Core Team. 2014. R version 3.1.0. R. A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Read, T. R., and S. M. Bellairs. 1999. Smoke affects the germination of native grasses of New South Wales. Australian Journal of Botany 47:563–576.

Reiner, R. J. 2007. Fire in California grasslands. Pages

207–217 *in* M. R. Stromberg, J. D. Corbin, and C. M. D'Antonio, editors. California grasslands: ecology and management. University of California Press, Berkeley, California, USA.

Reynolds, C. J., R. L. Long, G. R. Flematti, H. Cherry, and S. R. Turner. 2014. Karrikins promote germination of physiologically dormant seeds of *Chrysanthemoides monilifera* ssp. *monilifera* (boneseed). Weed Research 54:48–57.

Schoennagel, T., E. A. H. Smithwick, and M. G. Turner. 2008. Landscape heterogeneity following large fires: insights from Yellowstone National Park, USA. International Journal of Wildland Fire 17:742–753.

Seabloom, E. W., O. N. Bjørnstad, B. M. Bolker, and O. J. Reichman. 2005. Spatial signature of environmental heterogeneity, dispersal, and competition in successional grasslands. Ecological Monographs 75:199–214.

Shannon, C. E. 1948. A mathematical theory of communication. Bell System Technical Journal 27:623–656.

Stoll, P., and D. Prati. 2001. Intraspecific aggregation alters competitive interactions in experimental plant communities. Ecology 82:319–327.

Stromberg, M. R., T. P. Young, J. Wirka, and P. R. Kephart. 2007. California grassland restoration. Pages 254–280 *in* M. R. Stromberg, J. D. Corbin, and C. M. D'Antonio, editors. California grasslands: ecology and management. University of California Press, Berkeley, California, USA.

Swiecki, T. J., and E. Bernhardt. 1998. Effects of fire on naturally occurring blue oak (*Quercus douglasii*) saplings. Seventh workshop on seedling physiology and growth problems in oak plantings. September 27–29, 1998, South Lake Tahoe, California. USDA Forest Service North Central Research Station, St. Paul, Minnesota, USA.

Tilman, D. 1985. The resource-ratio hypothesis of plant succession. American Naturalist 125:827–852.

Veblen, K. E., K. A. Holmes, and T. P. Young. 2007. Response of one-year-old planted native grasses to controlled burns (California). Ecological Restoration 25:50–51.

Watt, A. S. 1947. Pattern and process in the plant community. Journal of Ecology 35:1–22.

Wills, R. 2006. Central Valley bioregion. Pages 295–320 *in* N. Sugihara, J. W. van Wagtendonk, K. E. Shaffer, J. Fites-Kaufman, and A. E. Thode, editors. Fire in California's ecosystems. University of California Press, Berkeley, California, USA.

Young, S. L., J. N. Barney, G. B. Kyser, T. S. Jones, and J. M. DiTomaso. 2009. Functionally similar species confer greater resistance to invasion: implications for grassland restoration. Restoration Ecology 17:884–892.

Yurkonis, K. A., and T. P. McKenna. 2014. Aggregating species at seeding may increase initial diversity during grassland reconstruction. Ecological Restoration 32:275–281.