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Fire and competition in a southern California grassland: impacts on the rare forb *Erodium macrophyllum*

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Summary

1. The use of off-season burns to control exotic vegetation shows promise for land managers. In California, wildfires tend to occur in the summer and autumn, when most grassland vegetation is dormant. The effects of spring fires on native bunchgrasses have been examined but their impacts on native forbs have received less attention.
2. We introduced *Erodium macrophyllum*, a rare native annual forb, by seeding plots in 10 different areas in a California grassland. We tested the hypotheses that *E. macrophyllum* would perform better (increased fecundity and germination) when competing with native grasses than with a mixture of exotic and native grasses, and fire would alter subsequent demography of *E. macrophyllum* and other species' abundances. We monitored the demography of *E. macrophyllum* for two seasons in plots manually weeded so that they were free from exotics, and in areas that were burned or not burned the spring after seeding.
3. Weeding increased *E. macrophyllum* seedling emergence, survival and fecundity during both seasons. When vegetation was burned in June 2001 (at the end of the first growing season) to kill exotic grass seeds before they dispersed, all *E. macrophyllum* plants had finished their life cycle and dispersed seeds, suggesting that burns at this time of year would not directly impact on fecundity. In the growing season after burning (2002), burned plots had less recruitment of *E. macrophyllum* but more establishment of native grass seedlings, suggesting burning may differentially affect seedling recruitment.
4. At the end of the second growing season (June 2002), burned plots had less cover of exotic and native grasses but more cover of exotic forbs. Nevertheless, *E. macrophyllum* plants in burned plots had greater fecundity than in non-burned plots, suggesting that exotic grasses are more competitive than exotic forbs.
5. A glasshouse study showed that exotic grasses competitively suppress *E. macrophyllum* to a greater extent than native grasses, indicating that the poor performance of *E. macrophyllum* in the non-burned plots was due to exotic grass competition.
6. *Synthesis and applications.* This study illustrates that fire can alter the competitive environment in grasslands with differential effects on rare forbs, and that exotic grasses strongly interfere with *E. macrophyllum*. For land managers, the benefits of prescribed spring burns will probably outweigh the costs of decreased *E. macrophyllum* establishment. Land managers can use spring burns to cause a flush of native grass recruitment and to create an environment that is, although abundant with exotic forbs, ultimately less competitive compared with non-burned areas dominated by exotic grasses.

Key-words: *Avena fatua*, *Nassella pulchra*, prairie, prescribed burns, restoration, split-plot design

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Introduction

The role of fire in grasslands and savannas is well recognized and can be either beneficial or detrimental. For example, Australian savannas are burnt approximately every 1–3 years to maintain biodiversity (Setterfield 2002). In contrast, in many ecosystems fire, coupled with invasive species, can perpetuate a positive grass–fire feedback cycle that can result in the decline of native species (D'Antonio & Vitousek 1992). In California and other areas in the western USA, fires are controversial

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because of the encroachment of suburban development into wildlands, but they are quickly becoming recognized as an inescapable component of land management for reducing fuel loads (Faulkner, Clebsch & Sanders 1989) and possibly for managing invasive species (DiTomaso, Kyser & Hastings 1999).

California grasslands have experienced one of the most dramatic biological invasions in North America, with an almost complete vegetation conversion from native annuals and perennials to exotic annual species (Mooney, Hamburg & Drake 1986; Heady 1990; Hamilton 1997). Introduced grasses and forbs are well known for their impact on native species, often through competitive interference (Dyer & Rice 1997; Holmes & Cowling 1997; Hamilton, Holzapfel & Mahall 1999; Carlsen, Menke & Pavlik 2000). Restoring invaded grasslands generally requires two strategies: (i) re-establishing native species and (ii) eliminating or decreasing the abundance of highly competitive exotic species.

Reintroduction of natural disturbance regimes through the use of grazing or fire is often used to restore grasslands (Russell-Smith *et al*. 1998; Hatch *et al*. 1999; Roques, O'Connor & Watkinson 2001; Brockway, Gatewood & Paris 2002). These methods attempt to decrease the abundance of introduced grasses and forbs while facilitating the recovery of native grasses and forbs. The success of grassland restoration is usually gauged by the increase in abundance of native perennial grasses (Dyer & Rice 1997; Hatch *et al*. 1999) but the effects of such restoration efforts on native forbs usually go unnoticed, despite the fact that forbs are a significant component of California grasslands (Heady 1990; Stromberg, Kephart & Yadon 2001). In fact, the importance of native forbs may be underappreciated in many grasslands and savannas as many studies focus on grasses and/or trees (Lamont, Witkowski & Enright 1993; Hoffman 1996; Higgins, Bond & Trollope 2000). However, forbs have received more attention with regard to diversity management in other areas, such as the tallgrass prairie in the USA (Briggs & Knapp 2001; Suding & Goldberg 2001; Brockway, Gatewood & Paris 2002) and grasslands in Sweden (Milberg 1994; Lennartsson & Oostermeijer 2001). Grassland forb communities are also of special interest because they represent a large proportion of rare and endangered grassland species (Kephart & Paladino 1997; Tecic *et al*. 1998; Tibor 2001). We know little about the impacts of grassland restoration efforts and invasive species on native forb communities, yet this information is critical if we are to understand how to conserve and restore the diversity of invaded grasslands.

The seasonality of fires can determine the resultant plant community (Parsons & Stohlgren 1989; Sparks & Masters 1996; Collins *et al*. 1998; Meyer & Schiffman 1999; Briggs & Knapp 2001; Main & Barry 2001). The use of prescribed fire outside the normal burn season is controversial because of the vegetation changes this may cause. However, restoration of some grasslands with prescribed burning shows promise because it can be applied on large scales with minimal investment. Most California grassland restoration studies using fire have utilized prescribed burns in the autumn (Dyer & Rice 1997; Hatch *et al*. 1999; but see Meyer & Schiffman 1999). Although this may coincide with historical fire seasonality, it does little to kill exotic species' seeds or vegetative parts because they are dormant in the autumn. If burns are carried out in the spring they are more likely to kill seeds of exotic species before they dehisce from their parent plant. Interestingly, there has been little research using prescribed burns in California grasslands in seasons other than autumn, even though burning in the spring may be more effective (DiTomaso, Kyser & Hastings 1999; Meyer & Schiffman 1999). Most studies have focused on dominant exotic and native grassland species, but the impacts of off-season burning on the diverse forb community is less well understood.

One forb of concern is *Erodium macrophyllum* Hook and Arn. (large-leaved filaree; Geraniaceae), a rare, native annual California grassland forb ranging from northern Baja, California, to southern Oregon. Since 1980, only 30 populations of *E. macrophyllum* have been documented throughout its entire range (Gillespie 2003), although it was once common in many areas of California (Gray 1876). Population sizes of *E. macrophyllum* range from approximately six to > 1000 individuals. The probable reasons for its decline are habitat loss, invasion by exotic species, grazing and off-highway vehicle activity (Gillespie 2003). Like most Californian annual grassland species, *E. macrophyllum* seeds germinate at the onset of winter rains and its basal rosette grows until the end of the spring, when it bolts, reproduces and then senesces before summer. Given its similar phenology to other native California forbs, *E. macrophyllum* makes a good model species to study competition and fire and their effects on native forbs.

Demographic studies can identify which life-history processes may be especially critical for a plant's success (Fiedler 1987; Pavlik & Espeland 1998; Gregory *et al*. 2001) and for developing management plans (Schemske *et al*. 1994; Kirkman, Drew & Edwards 1998; Lesica 1999). By understanding how restoration practices differentially affect demographic parameters such as establishment, growth and reproduction, we can better adapt such restoration efforts to accommodate the rare plants in question. For example, if restoration practices such as burning result in increased fruit production but negatively impact establishment, the costs and benefits of the restoration can be weighed appropriately.

The purpose of the current study was to investigate how prescribed spring burns and exotic species in a southern California grassland impact the grassland community. We specifically examined how prescribed burns and competition with exotic species impacted the demography of the rare forb *E. macrophyllum*. Additionally, we monitored changes in plant groups (native grasses, native forbs, exotic grasses and exotic forbs) in response to burning and competition treatments.

Materials and methods

STUDY SITE DESCRIPTION

The study was carried out at the Santa Rosa Plateau Ecological Reserve (33°31′N, 117°15′W, 600 m a.s.l.) in western Riverside County, California, USA. The reserve comprises chaparral, oak woodlands, native and exotic grasslands and coastal sage scrub. The soils are primarily derived from decomposed basalt. The climate is mediterranean, with cool, wet winters and hot, dry summers. Almost all precipitation occurs between November and April. Annual precipitation during the 2000–01 season (from July to June) was 28·7 cm, and just 9·8 cm during the 2001–02 season. The average is 48 cm annual precipitation.

The experiment was conducted along a 2-km stretch of grasslands near Monument Hill Road in the south-eastern part of the reserve. This portion of the reserve was selected because, during the time the study took place, it was in an area designated for prescribed burns. The Santa Rosa Plateau Ecological Reserve has large areas where *Nassella pulchra* (native grass) is dominant. Growing in the interspaces between *N. pulchra* are common mediterranean annual grasses, *Avena* spp., *Bromus diandrus*, *Bromus hordeaceous*, *Bromus madritensis* and *Vulpia myuros*. (All nomenclature follows Hickman 1993).

EXPERIMENTAL DESIGN

We used a two-factor split-plot design, with subplots replicated five times within each main plot. Main plots were either burned or non-burned (replicated five times) and subplots were weeded or non-weeded (replicated 50 times). Burned and non-burned areas were located along a 2-km stretch of Monument Hill Road in areas that were nearly level. The burning treatment was not paired because of limitations in the availability of level areas and restrictions on which areas were allowed to be burned by the land managers. In each burned area an array of 10 1 × 0·5-m subplots (10 main plots × 10 subplots = 100 subplots) was established permanently. Half-metre square subplots are an appropriate size because naturally occurring densities of *E. macrophyllum* can reach > 100 seedlings m^{-2} and more than 15 adults m^{-2} and similar plot sizes have been adequate for studying other species of *Erodium* (Rice 1987). The weeding treatment was randomly assigned to five of the 10 subplots in each larger burned or non-burned plot. Each of the larger 10 main plots were approximately 40 × 40 m, but size varied because it was determined by the edges to which the fires burned. For each burned main plot, the subplots were always at least 5 m from the burn edge to minimize any possible edge effects.

Subplots were chosen on the basis of two criteria: (i) they contained at least three adults of the native perennial bunchgrass *N. pulchra* and (ii) they had mainly exotic grasses (as opposed to exotic forbs) growing in the interspaces between *N. pulchra* plants. In two of the main non-burned plots, gypsum blocks (Model GB-1; Delmhorst, Towaco, NJ) were installed 15 cm below the soil surface in both weeded and non-weeded subplots (10 replicates in each treatment). These were used to measure soil moisture throughout the duration of the experiment. In March 2001, to calibrate the gypsum blocks, soil samples were collected from a depth of 15 cm adjacent to the gypsum blocks, sealed in small plastic bags, put on ice and transported back to a laboratory. The water potential of the soil samples were computed using a WP4 Dewpoint Potentiometer (Decagon, Pullman, WA) and a regression of soil water potential vs. gypsum block readings was computed.

During November 2000 we manually removed all exotic species from the subplots that were to receive the weeding treatment. However, because very little rainfall had occurred at this time, there were few exotics to remove. A 15-cm border was also weeded around each subplot. Weeding was done throughout the growing season as needed, but exotic emergence was sparse after the initial weeding. Living weeded plant material was removed from the subplots and discarded at least 1 m away, while as much as possible of the remnant exotic species litter (thatch) was left in the subplots to minimize differences in microenvironments between the weeding treatment and control. Most of the species weeded were either *B. madritensis*, *B. hordeaceous*, *Avena* sp., *V. myuros* or *Erodium botrys.* However, in some of the subplots *Silene gallica*, *Lactuca seriola* and *Sonchus apser* were also weeded. The mean exotic seedling density in the weeded subplots was 2860 ± 563 (SE) m^{-2} (counted in a subsample, $n = 14$). In early January 2001, before the onset of major winter rains, 200 seeds of *E. macrophyllum* were broadcast into each of the 100 subplots. The seeds came from plants reared in a glasshouse during summer 2000. The original seed source came from a natural population of *E. macrophyllum* approximately 15 km away from the study site. During the 2000–01 growing season, all plots were monitored weekly. When a germinating *E. macrophyllum* was observed it was marked with a numbered wooden toothpick placed on the north side of plants to prevent any shading. All *E. macrophyllum* plants were monitored until the end of the growing season in May 2001, as described below.

In autumn of 2001 all exotic species were again manually removed from the weeded subplots. During this second season (2001–02) there were still high densities of exotic species germinating in the plots despite the removal treatments the previous year. This was probably due to the residual seed bank and seed rain from exotic species outside the subplots, despite the 15-cm weeded edge. During the 2001–02 season, 10 randomly selected *E. macrophyllum* plants per plot were marked with toothpicks after a large recruitment period because higher densities made it impractical to mark and follow each individual. However, total numbers of emerged seedlings of *E. macrophyllum* were counted so that we could calculate percentage establishment for each subplot.

During this season plants were monitored every 10–14 days.

PRESCRIBED BURNING

Burning took place on 13 June 2001. Around each of the five plots to be burned a 2-m path was hand cut to reduce the risk of the fire 'jumping' out of the burn plots. Before ignition, the path around the burn area was dampened with water. The fire was started by lighting the downwind edges of the burn area so that fire burned from the edges towards the centre of the plot. On the day of the burn, the temperature was approximately 28 °C, relative humidity 59% and wind speed 4 knots out of west, north-west. At the time of burning, many exotic grass seeds had not dispersed but *E. macrophyllum* had completely senesced.

DATA COLLECTION AND MONITORING

During both the 2000–01 and 2001–02 field seasons (from here on referred to as the 2001 and 2002 seasons, respectively), *E. macrophyllum* plants in each subplot were monitored by first locating each plant associated with its numbered toothpick and then assessing its phenological state. At the end of both growing seasons, mature fruits on flagged *E. macrophyllum* plants were counted to assess fecundity. Accurate counts of total fruits produced per plant were possible, even though *E. macrophyllum* can continually produce fruit over several weeks (I. Gillespie, unpublished data), because the elongated style from each fruit remains on the plant after seed dispersal.

During the 2002 growing season we also measured density of *N. pulchra* seedlings in all 100 subplots. *Nassella pulchra* density was estimated by placing a 10 × 10 cm quadrat three times at approximately 17-cm intervals within the centre of each subplot and counting the number of *N. pulchra* seedlings within the quadrat. *Nassella pulchra* seedlings had less than five leaves and were easily distinguishable from resprouting adults because of the absence of burned tillers.

We also estimated percentage cover of plant groups in each subplot: native grasses, native forbs, exotic grasses and exotic forbs, as well as *E. macrophyllum*. Percentage cover of each group was estimated visually by placing a metal frame with 10-cm tick marks around its edges on the subplot. To minimize error, visual estimates were always made by the same person. Data collection for percentage cover of plant groups occurred over a 2-day period in March 2002. Although density of annuals can fluctuate from year to year, the difference in percentage cover of plant groups due to annual variation is much less than differences caused from treatment effects. Further, the relative contribution of cover from different plant groups (exotic and native forbs, and exotic and native grasses) remains approximately the same within seasons (I. Gillespie, personal observation) so we felt confident that this one-time sampling gave a general synopsis of species' cover. Native forbs (excluding *E. macrophyllum*) were sparse in the study plots throughout the course of this experiment.

MICROCLIMATIC DATA

During the 2002 growing season we recorded soil surface temperature and irradiance [photosynthetic photon flux density (PPFD; 400–700 nm)] in both weeded and non-weeded subplots in both burned and non-burned main plots. Soil surface temperature was recorded by placing soil temperature sensors approximately 1 cm below the soil surface in the centre of each subplot. The sensors were connected to HOBO data loggers (Onset, Bourne, MA) programmed to collect and store temperature readings at 30-min intervals. All treatments were measured within three consecutive days from 30 January to 2 February 2002. Instantaneous irradiance was measured on 22 March 2002 from 11:00 to 12:00 hours by placing a light sensor (Model Li-1000; LiCor, Lincoln, NE) in the centre of each subplot at ground level. Irradiance measurements were recorded from all subplots within three randomly chosen burned and non-burned plots.

GLASSHOUSE COMPETITION EXPERIMENT

We conducted a glasshouse experiment to analyse the competitive effects of *N. pulchra* and *Avena fatua* on *E. macrophyllum* biomass accumulation. We used a seven-factor randomized block design replicated five times. Treatments were three different densities of *A. fatua* and *N. pulchra* surrounding a single *E. macrophyllum* seedling, or *E. macrophyllum* growing without any competition (control). The densities were two, four or six competitors surrounding a single *E. macrophyllum* target seedling. All seedlings were carefully transplanted into plastic pots on 20 May 2002 [30 cm diameter, 28 cm deep; University of California soil mix no. 3 slow nutrient release (56% sand, 44% peat moss; 0·256 kg m^{-3} KNO_3, 0·256 kg m^{-3} K_2SO_4, 1·32 kg m^{-3} $Ca(H_3O_4P)_2$)], approximately 4 days after germinating. The *E. macrophyllum* seedling was transplanted into the centre of the pot with the appropriate density of competitors transplanted at equal distance from each other, *E. macrophyllum* and the outer edge of the pot. The pots were watered to field capacity every other day via drip irrigation. The daytime temperature of the glasshouse was kept at approximately 26 °C and photosynthetic active radiation was approximately two-thirds of the ambient light intensity outside. On 2 July 2002 we measured height and width of all *E. macrophyllum* plants and harvested above-ground biomass. Height was measured from the soil surface to the top of the highest point; width of each plant was measured at its widest point. Above-ground parts were oven dried for 36 h before their mass was obtained.

DATA ANALYSIS

To test for treatment effects for both growing seasons we used a two-way ANOVA modified for a split-plot design with replicated subplots. To accommodate different levels of replication for both treatments we could not use the residual means squares as the denominator for all *F*-tests. To test the fire treatment, fire nested within plot was used as the denominator, but for the weeding and fire × weeding interaction the residual error term was used as the denominator. For 2001, even though the fire treatment had not been applied, we still used the two-way ANOVA described above to test for any inherent differences in the burned and non-burned plots.

Fruit production per plant data and *N. pulchra* density data were $\log(x + 1)$ transformed. Percentage establishment was calculated as the total number of establishing/emerging seedlings divided by the number of potential seeds in soil. During the 2002 growing season the potential number of seeds in the soil comprised seeds left in the seed bank from autumn–winter 2001 plus any seeds added by reproduction in spring of 2001. Therefore, in 2002, percentage establishment per subplot was calculated as total number of seedlings established or emerged/(number of total potential seeds left in the soil per subplot in 2001 + number of seeds added from reproduction during spring 2001).

Soil surface temperature and irradiance data were analysed using a two-way ANOVA; day was a blocking factor for soil temperature analyses. For the glasshouse experiment, we used a one-way ANOVA to test the treatment effects on plant height-to-width ratios and shoot biomass.

All analyses were done using Stata 7·0 (Stata Corporation, College Station, TX) running on Mac OS X 10·1. Means ± one SE are reported throughout and $P < 0·05$ is considered significant.

Results

WEEDING AND FIRE EFFECTS ON *E. MACROPHYLLUM*

During 2001 recruitment of *E. macrophyllum* was episodic, occurring from January to April 2001. Flushes of establishment coincided with pulses of rainfall. In the 2002 season, however, recruitment was limited entirely to the month of December 2001. During both growing seasons weeded subplots had greater percentage establishment (2001, $F_{1,88} = 14·11$, $P < 0·001$; 2002, see Table 1 and Fig. 1a). During 2001, mean percentage establishment in weeded subplots was 4·3 ± 0·3% and mean percentage establishment in non-weeded subplots was 3·0 ± 0·2%.

During the 2002 season overall percentage establishment was almost six times greater than the year before (3·6 ± 0·2% for 2001 and 21·3 ± 1·1% for 2002). During the second season after the fire treatment had been applied, burned plots had significantly less percentage establishment than non-burned plots (Table 1 and Fig. 1a). There was no difference in percentage cover of *E. macrophyllum* between burned and non-burned treatments, but weeding had a strong effect (Table 1 and Fig. 1b).

In both years, removal of exotics resulted in an increase in fruit production per plant (for 2001 $F_{1,88}$, $P < 0·0001$; for 2002 see Table 1 and Fig. 1c). For 2002, the burning treatment significantly increased fruit production per plant (Table 1 and Fig. 1c).

Burning did not directly affect *E. macrophyllum* plants because they had finished their reproductive cycle before the fires were set. However, burning caused vegetative damage to several late-season native forbs (*Calystegia macrostegia*, *Calochortus splendens*, *Eremocarpus setigerus*, *Erigeron* sp. and *Gnaphalium californicum*) and exotic forbs (*Sonchus asper*, *E. botrys*, *Erodium moschatum*, *Gnaphalium luteo-album* and *Hirschfeldia incana*).

EFFECTS OF WEEDING AND FIRE ON PLANT GROUPS AND *N. PULCHRA* DENSITY

Weeding increased the percentage cover of native grass ($F_{1,88} = 21·28$, $P \leq 0·0001$), while fire decreased its cover ($F_{1,8} = 12·81$, $P = 0·0072$); there was no significant interaction effect. Neither the weeding nor fire treatment affected the percentage cover of native forbs. Manual weeding of exotic grasses and forbs reduced their mean percentage cover from 22·2 ± 3·3 to 1·22 ± 0·2 and 28·3 ± 3·3 to 8·0 ± 1·2, respectively. There were drastic differences in percentage cover of all groups (except native forbs) between the non-weeded, burned and non-burned

Table 1. Effects of fire and weeding on *Erodium macrophyllum* establishment, cover, fecundity and *Nassella pulchra* seedling density in spring of 2002. ANOVA table shows set up to accommodate for a split-plot design with replicated subplots. For direction of effects refer to Fig. 2 for *E. macrophyllum* and text for *N. pulchra*

		Erodium macrophyllum						*Nassella pulchra*	
		Establishment		% cover		Fecundity		Seedling density	
Treatment	d.f.	MS	*P*	MS	*P*	MS	*P*	MS	*P*
Fire	1	2035	< 0·001	6·76	0·675	1·126	0·011	2·053	0·024
Plot(fire)	8	189		35·81		0·0158		0·267	
Weed	1	1092	< 0·001	750·76	< 0·001	0·226	< 0·001	0·888	0·001
Fire × weed	1	91	0·006	1·96	0·687	0·126	0·313	0·015	0·661
Residual	88	89		22·23		0·016		0·121	

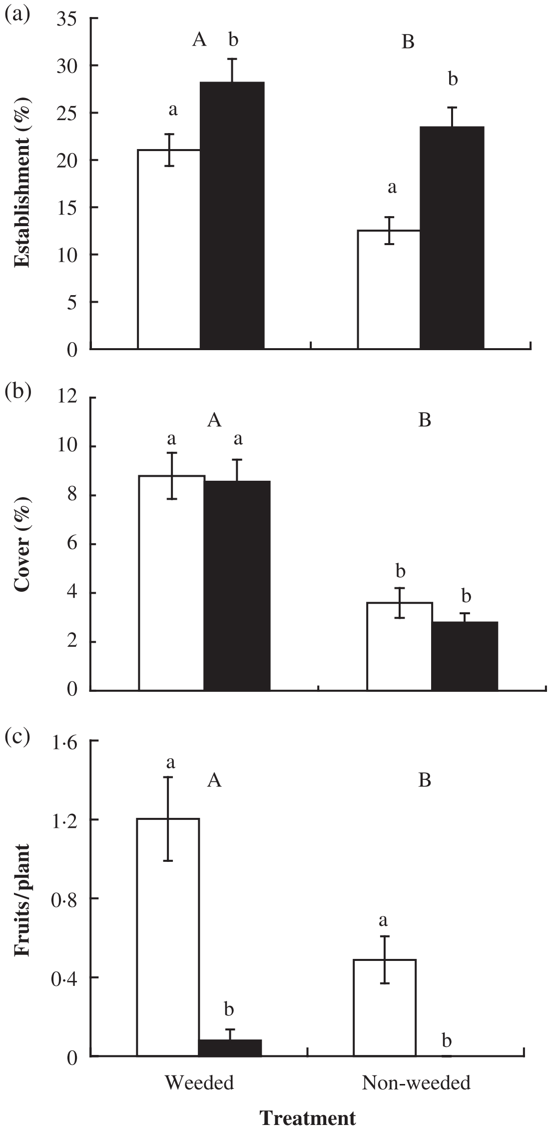

Fig. 1. Establishment (a), percentage cover (b) and fecundity (c) of *Erodium macrophyllum* growing in weeded and non-weeded subplots in burned and non-burned areas in 2002. Clear bars are burned subplots and solid bars are non-burned subplots. Different non-bold capital letters indicate a significant difference between the weeding treatment, lower case letters indicate difference between burning treatment and interaction effects. Data are means ± SE.

subplots (Fig. 2). For the burned, non-weeded subplots, there was 7·8% less cover of native grasses and 35·4% less cover of exotic grasses. In contrast, burned, non-weeded subplots had 30·2% more cover of exotic forbs than non-burned, non-weeded subplots. Exotic forbs consisted almost entirely of *E. botrys*.

There was very low percentage cover of native forbs in all treatments (Fig. 2). Similarly, density of native forbs was extremely low; rarely was more than one native forb per subplot found (except for *E. macrophyllum*). The native forbs occurring in the subplots were *Calystegia macrostegia*, *Dichelostemma capitatum*, *Eremocarpus setigerus*, *Plagiobothrys* sp., *Sidalcea malviflora* and *Viola pedunculata.*

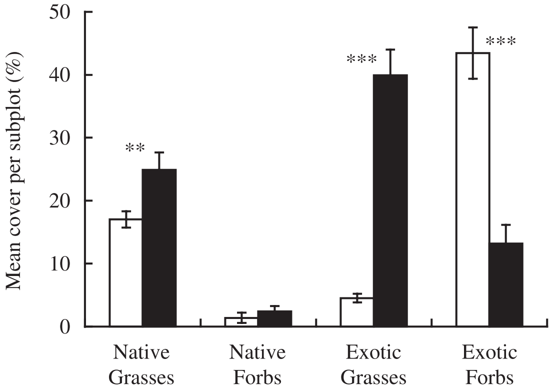

Fig. 2. Differences in percentage cover of functional groups between non-weeded burned and non-burned subplots. Clear bars are burned subplots and solid bars are non-burned subplots. Data are means ± SE from 2002 season. $^{**}P < 0{\cdot}01$ and $^{***}P < 0{\cdot}001$.

Both weeding and burning increased *N. pulchra* seedling density. Weeding increased seedling density from 9·4 seedlings m^{-2} to 16·1 seedling m^{-2}, and burning increased density from 8·1 seedlings m^{-2} to 17·3 seedlings m^{-2} (Table 1). There was no interaction effect.

MICROCLIMATE

Fire increased mean soil temperature ($F = 61{\cdot}54$, $P < 0{\cdot}001$) while weeding had no effect. There was also a day effect ($F = 3{\cdot}75$, $P = 0{\cdot}024$). A mean maximum soil temperature of 24·1 °C was reached in the weeded, burned plots at approximately 12:00 hours. Burned, non-weeded subplots had the second highest temperature (22·7 °C), reached at approximately the same time. Weeded, non-burned subplots were the third warmest (19·2 °C), followed by the non-weeded, non-burned subplots (16·0 °C). The differences in mean soil temperature among treatments were fairly consistent throughout the days over which they were averaged.

Both the weeding and fire treatments increased irradiance in the subplots. The weeding treatment increased light intensity from 945 µmol photons m^{-2} s^{-1} to 1218 µmol photons m^{-2} s^{-1} ($F_{1,56} = 5{\cdot}57$, $P = 0{\cdot}021$) and the fire treatment from 816 µmol photons m^{-2} s^{-1} to 1348 µmol photons m^{-2} s^{-1} ($F_{1,56} = 21{\cdot}21$, $P < 0{\cdot}001$). There was also an interaction effect where burned, non-weeded plots had greater irradiance than would have been predicted by the relative effects of weeding and burning alone ($F_{1,56} = 5{\cdot}51$, $P = 0{\cdot}023$). Weeded and non-weeded, burned subplots had very similar mean levels of incident radiation (PPFD) reaching the soil surface (1349 µmol photons m^{-2} s^{-1} and 1347 µmol photons m^{-2} s^{-1}, respectively). Weeded, non-burned subplots had the next highest level of PPFD (1088 µmol photons m^{-2} s^{-1}) and the most shaded subplots were the non-weeded, non-burned subplots (544 µmol photons m^{-2} s^{-1}). Soil water potential in 2001 ranged from –0·5 to –1·9 MPa, and in 2002 from –0·6 to –1·9 MPa. For both years, we were unable to detect a difference in soil water potential between weeded and non-weeded plots.

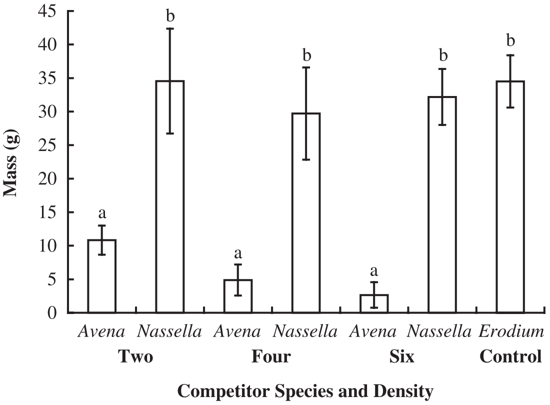

Fig. 3. Shoot biomass of *Erodium macrophyllum* growing with different competitors at three different densities (two, four and six competitors per pot). *Erodium* control is *E. macrophyllum* growing without competitors. Different letters indicate significant differences ($P < 0{\cdot}001$) between treatments. Data are means ± SE ($n = 5$).

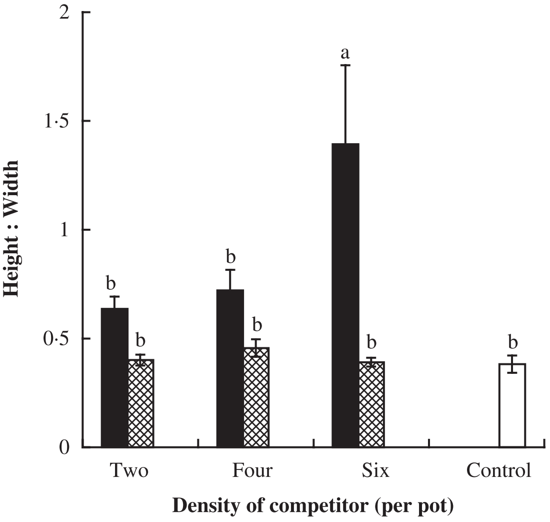

Fig. 4. Comparison of height–width ratios of *Erodium macrophyllum* growing with two different competitors at three different densities (two, four and six competitors per pot). Solid dark bars are *E. macrophyllum* growing with *Avena fatua*, hatched bars are with *Nassella pulchra* and the clear bar is *E. macrophyllum* growing without competitors. Different letters indicate significant differences ($P < 0{\cdot}01$) between treatments. Data are means ± SE ($n = 5$).

GLASSHOUSE COMPETITION EXPERIMENT

All densities of *A. fatua* decreased the biomass of *E. macrophyllum* (Fig. 3) compared with *E. macrophyllum* growing without competitors. There was no difference in biomass accumulation between *E. macrophyllum* growing with three densities of *N. pulchra* vs. *E. macrophyllum* growing alone. *Erodium macrophyllum* growing with a density of six *A. fatua* plants per pot resulted in the largest height–width ratio. No other competitors at either of the three densities had an effect on *E. macrophyllum* height–width ratio (Fig. 4).

Discussion

Our results indicate that *E. macrophyllum* performed better in a grassland dominated only by native species compared with a grassland supporting both native and exotic species. Although high densities of native bunchgrasses may not be beneficial for native forbs, our results indicate they are still not as competitive as exotic grasses; our glasshouse study demonstrated that the exotic grass *A. fatua* greatly impacted biomass accumulation of *E. macrophyllum* compared with *N. pulchra*. In a similar experiment, the endangered forb *Amsinckia grandiflora* had greater reproductive output when grown in plots with *Poa secunda* (native perennial grass) than in plots dominated by exotic grasses of equivalent biomass (Carlsen, Menke & Pavlik 2000). The prescribed spring burns in this study drastically reduced the cover of invasive grasses, similar to the levels achieved by hand weeding. This reduction in invasive grasses is presumably the mechanism that allowed for greater reproductive output of *E. macrophyllum* in burned plots.

Burning increased establishment of *N. pulchra* seedlings and decreased exotic grass cover. Burned subplots had almost three times as many *N. pulchra* seedlings as non-burned subplots. While this may be good for *N. pulchra*, increased densities of perennial grasses may not be beneficial for native forbs (Edwards 1994; Carlsen, Menke & Pavlik 2000). Given that prescribed burns can increase native bunchgrass density (Dyer, Fossum & Menke 1996) and that high densities of native bunchgrasses may competitively suppress rare native forbs, a balance must be found between the beneficial impacts of prescribed fires on reducing exotic annual grasses and the potential negative indirect impacts they have on rare forbs. Although our glasshouse study suggests that *N. pulchra* seedlings do not competitively suppress *E. macrophyllum*, adult *N. pulchra* plants at similar densities may be more competitive.

Burning had strong effects on percentage cover of plant functional groups (native grasses, native forbs, exotic grasses and exotic forbs). Although burning reduced the cover of native grasses (*N. pulchra*) after 1 year, in subsequent years it will probably increase in the burned subplots (Parsons & Stohlgren 1989; DiTomaso, Kyser & Hastings 1999). Exotic grasses were effectively replaced with exotic forbs in the interspaces between adult *N. pulchra* plants in the burned subplots. This means that when *E. macrophyllum* was growing in non-weeded, burned plots it was growing with (and presumably competing with) *N. pulchra* and *E. botrys*, whereas in the non-weeded, non-burned subplots *E. macrophyllum* was growing with *N. pulchra* and exotic grasses. The exotic forbs found in the subplots were almost entirely *E. botrys*. *Erodium botrys* (and *Erodium brachycarpum*) have increased germination rates and fitness in areas that are clear of thatch (Rice 1985). The decrease in litter from the burning and the subsequent greater fluctuations in soil temperature probably facilitated exotic *Erodium* recruitment (Rice 1985). Despite the widespread occurrence and dominance of several exotic *Erodium* spp. in California grasslands (Hickman 1993), the impacts they have on native species has received little attention even though they can germinate in high densities, especially when soil temperatures fluctuate (Rice 1985). Our results suggest that exotic *Erodium* spp. have a smaller competitive impact on *E. macrophyllum* than exotic grasses, because non-weeded, burned subplots (dominated by exotic *Erodium*) had greater fruit production than the non-weeded, non-burned subplots (dominated by exotic grass).

Fires alter the microclimate by reducing dead and living biomass. This in turn can alter soil temperature, light intensity and soil nutrients (Vogl 1974; Gimeno-Garcia, Andreu & Rubio 2000). It is possible that changes in these parameters may have been the mechanism driving the differences we found in increased seedling establishment of *N. pulchra* and decreased establishment of *E. macrophyllum*. These results are similar to those of Hoffman (1996) in a neotropical savanna in Brazil, where fire and litter removal had contrasting effects on seedling establishment for different species. However, weeding resulted in an increase in seedling establishment of *E. macrophyllum*. Even though weeding and burning can similarly alter the microenvironment through their effects on light intensity and soil temperature, they are apparently different enough to cause differential *E. macrophyllum* recruitment. An alternative hypothesis is that the fire may have burned seeds of *E. macrophyllum* and thus indirectly decreased establishment. However, this may be unlikely for two reasons. First, the awns on seeds of *E. macrophyllum* can coil and expand in response to changes in moisture and effectively drill them into the ground (Zomlefer 1994). thereby increasing the likelihood that seeds will escape the heat from a fire. Secondly, we found the congener *E. botrys* to have extremely high seedling densities following prescribed burns, indicating that at least some species in the genus *Erodium* respond positively to fire. Regardless, further experimentation is necessary to understand the mechanism that causes changes in establishment of *E. macrophyllum* following weeding and prescribed burns.

A question of central concern to this study is how prescribed spring burns impact the forb community (in addition to *E. macrophyllum*) at the Santa Rosa Plateau Ecological Reserve. Neither weeding nor burning had an effect on subsequent cover in native forbs (excluding *E. macrophyllum*). This is in contrast to what others have found in grasslands in other locations of California, where prescribed burning increased native forb abundance (Parsons & Stohlgren 1989; DiTomaso, Kyser & Hastings 1999; Meyer & Schiffman 1999). The lack of response in our study may be a function of the very little precipitation that fell during the year following the burn (2002). Alternatively, the native forb seed bank at the Santa Rosa Plateau Ecological Reserve may be low in the area where we had our study plots. Soil nutrients may also play a role in affecting forb diversity. However, given that fire can reduce soil nutrients (Debano & Conrad 1978) and that increasing nitrogen can reduce diversity (Vitousek *et al.* 1997), it seems likely that fire, through its alteration of soil nutrients, may promote forb diversity. We did not find this in our study, but 2 years after a fire may be too short a time to notice a difference if there is a depauperate forb seed bank.

Manual weeding is highly effective at reducing competitive effects, but it is not practical or economical over large areas. Exotic annual grasses and forbs often germinate at exceedingly high densities in the interspaces between native bunchgrasses (Hamilton, Holzapfel & Mahall 1999). Dense seedlings decrease light and available soil moisture (Dyer & Rice 1997). Over both years, approximately 90% of *E. macrophyllum* seedlings growing in non-weeded subplots died following emergence. These plants exhibited drought stress; symptoms included flaccid leaves and tissue necrosis on the leaf margins. It is likely that the cause of death was competition for water and light with exotic species. Although we did not find a difference in soil water potential between weeded and non-weeded subplots at a 15-cm depth, competition for below-ground resources (especially water) in California's mediterranean ecosystems can be a factor influencing native species (Eliason & Allen 1997; Hamilton, Holzapfel & Mahall 1999). Competition for light may cause decreased fecundity and/or growth of native species growing in a matrix of exotic grasses (Dyer & Rice 1999). In the glasshouse pot study at high densities (six *A. fatua* plants per pot), *E. macrophyllum* grew taller compared with its smaller height–width ratio when grown with *N. pulchra* or by itself. This suggests that, at high densities, *E. macrophyllum* was competing for light with exotic species. Importantly, light competition is reduced following fire, which is beneficial for *E. macrophyllum* fecundity.

Our research has several implications for grassland management and restoration. Although this study took place over approximately 4 km^2 of the reserve, the results can probably be applied to other grasslands within the reserve, as many share similar topographic, vegetative and soil characteristics. Similarly, the results are relevant, although perhaps not directly applicable, to grasslands off the reserve because many areas in California share the same invasive species as in this study and because *E. macrophyllum* was historically found throughout California. We have shown that exotic annuals strongly interfered with the rare forb *E. macrophyllum* by reducing recruitment, survival and fecundity. However, the use of fire for altering grassland habitat for restoration of *E. macrophyllum* had conflicting effects; fire resulted in increased fruit production per plant, but it also decreased establishment of *E. macrophyllum* seedlings. The benefits of increased fecundity may be realized in future years when absence of fire enables establishment. Additionally, it is possible that prescribed spring burns will have other effects on those forbs that disperse seed prior to the fire (DiTomaso, Kyser & Hastings 1999). The impacts of prescribed spring burns on late-season forbs is still an open question. For reseeding with native forbs, the effects of prescribed burns shows promise for reducing competition from exotic grasses, although the resultant increase in exotic forbs should not be overlooked.

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