COMPOSITION AND STRUCTURE OF A GRASSLAND COMMUNITY FOLLOWING PRESCRIBED BURNS ON SANTA CRUZ ISLAND

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ABSTRACT

A series of three prescribed burns varying in size from 270 to 490 hectares was done in grasslands on Santa Cruz Island between 1993 and 1995. The two main goals of the burns were to begin an evaluation of the effect of fire as an ecological process in the island's communities, and to determine if fire can be used as a restoration tool to enhance native plant species distribution and abundance in grasslands on Santa Cruz Island. Although total species richness and diversity tended not to change systematically as a result of burning, the postburn composition of the burned areas was significantly different from that of preburned conditions and unburned controls (matched to each burned plot by year). The response to burning varied between different vegetation guilds and within the different burn areas. Burned and unburned plots were dominated by alien grasses in all years, while the guild that tended to show the greatest positive response to the burns were annual forbs. By the third year postburn, the burned plots were beginning to return to a composition similar to preburn conditions. The richness and abundance of native species tended to either increase or remain unchanged as a result of the burning.

Keywords: Diversity, grasslands, fire, prescribed burns, Santa Cruz Island.

INTRODUCTION

Grasslands in California have undergone dramatic changes in composition and distribution over the last 200 years. Community composition has been severely altered by heavy grazing from domestic livestock and the introduction of alien plant species, leading to a conversion from communities dominated by native perennial bunchgrasses and forbs to ones comprised predominantly of alien annual grasses and forbs (Heady 1977; Bartolome et al. 1986; Mack 1989). Removing grazing pressure does not lead to a return of native perennial bunchgrasses or a reduction in abundance of alien grasses, so alien herbaceous species persist in grasslands throughout the state (White 1967; Bartolome and Gemmill 1981; Baker 1989). Compounding the problems of drastically altered grazing regimes and the influx of alien species has been the reduction in extent of native grasslands. Beginning in the middle to late twentieth century, the amount of natural grassland area in the state has been reduced by urbanization and agriculture. As a result of the combination of conversion from perennial to annual grassland and habitat loss, remnant patches of native perennial grassland usually exist now as small, isolated fragments.

Grassland communities on the California islands underwent a similar conversion as a result of severe overgrazing from feral and domestic livestock (Minnich 1980; Junak et al. 1995). The islands remain relatively undeveloped and loss of habitat has not been a serious problem, but alien herbaceous species dominate grassland communities, resulting in the distribution and abundance of native herbaceous species becoming more restricted than alien species (Klinger 1998). Programs to remove feral and domestic animals have been undertaken by most of the organizations managing the islands (Schuyler 1993; Halvorson 1994; Keegan et al. 1994), with the primary goal of enhancing and/or restoring the composition, structure and function of the natural communities. However, based on the patterns observed on the mainland, these removal programs will in all likelihood be only a first step in a much longer management process, and other types of programs will need to be tested and evaluated before an effective restoration protocol can be designed (Klinger et al. 1994; Laughrin et al. 1994).

Prescribed burning has been suggested as a potential tool for restoring native species to grassland communities and has been tested in several areas of California (Parsons and Stohlgren 1989; Dyer et al. 1996). The results of these experiments have been mixed; in the foothills of the Sierra Nevada the biomass of alien annual grass was reduced and the biomass of both alien and native forbs increased following three successive burns (fall or spring), but these effects were transient and were not sustained beyond the burning treatments (Parsons and Stohlgren 1989). At the Jepson Prairie, Dyer et al. (1996) found that recruitment of *Nasella* *pulchra* was relatively high in burned areas but was also highly dependent on variations in annual climatic conditions.

The historic role of fire on the structure and composition of plant communities on the California islands is poorly understood. Although it is generally accepted that fire was an important component of the islands' natural systems, and plant species on the islands have similar adaptations to fire as those on the mainland (Carroll et al. 1993), information is lacking on the historic fire regime. We know fire was suppressed over the last 150 years, both by human choice and lack of extensive fuels because of the severe overgrazing which had occurred, but we know little about aboriginal burning on the islands and less about naturally occurring fires. From a contemporary perspective, it is likely that fires on the islands will grow more frequent. They will be a result of a continuing increase in the extent and density of fuels, natural and accidental ignition (Carroll et al. 1993), prescribed burning and reduced suppression efforts (Wells 1991).

The contemporary role of fire has two aspects then: the first as a naturally occurring process in an ecological regime drastically different from historic ones, and the second as a restoration tool. These aspects are not necessarily exclusive, but must be evaluated by different criteria. It is recognized that the invasion of alien species can alter disturbance regimes (Mack and D'Antonio 1998), leading to different patterns of succession and composition in the disturbed communities. As more and more areas become impacted and altered by nonnative plants and animals, scientists and land mangers are trying to understand ecological processes from both an historical and contemporary perspective relative to these invasions. It is believed that by understanding the historic relationship of communities and their disturbance regimes, effective management tools can be developed for preserving the biological integrity of natural systems. Few truly natural systems exist any more, and for agencies responsible for the management of natural communities and their resources, determining what the outcomes will be of a natural process within the context of communities severely altered in composition and structure is an important undertaking.

In this study we used prescribed burning as a way of evaluating the role of fire on the structure, diversity, and composition of grasslands on Santa Cruz Island, and to evaluate the effectiveness of prescribed burning for creating conditions beneficial to native species in these communities. We chose to conduct the study in grasslands because of their extensive distribution on the islands, because alien species have had the greatest relative impact in these as opposed to other communities, and because the light, flashy fuels make grasslands the most likely areas for a fire to either start or be carried across an extensive part of the island.

STUDY AREA

The project was conducted in grasslands on the southwest side of Santa Cruz Island. A detailed description of the island is given in Junak et al. (1995). Soils in the southwest grasslands are derived mainly from shale and silt deposits and are cut with deep gullies as a result of locally severe erosion. Three relatively broad watercourses drain the area; Poso, Alegria, and Sauces creeks. The elevation ranges from 0 to 350 m, with the topography characterized by relatively steep hills (30 to 80% slope) dissected by numerous small drainages.

The two primary plant communities which occurred in the study area were grasslands and coastal scrub. Grasslands comprised over 80% of the area and were dominated by alien grasses (*Lolium multiflorum, Avena barbata, A. fatua*, *Bromus diandrus, B. mollis, B. rubens, Vulpia myuros*), with an interspersion of native shrubs (*Artemisia californica, Baccharis pilularis, Hazardia squarrosus, Rhus integrifolia*). Coastal scrub was dominated by native shrubs, alien grasses, and a combination of native and alien forbs (*Atriplex semibaccata, Dichelostemma capitatum, Erodium spp., Sanicula arguta, Sisyrinchium bellum)*. Relatively small patches of native grass (*Nasella pulchra*) occurred throughout the grasslands and coastal scrub communities.

METHODS

The study was conducted from the spring of 1993 to the spring of 1998. We selected three contiguous treatment areas of varying size and configuration to be burned and an adjacent unburned area to be a control (Table 1). One of the three treatment areas was burned each fall (early November to early December) from 1993 to 1995.

We monitored the effect of fire on herbaceous and woody species by sampling in the spring preceding each burn and then each spring for three years after. We collected data in 10 burned and 10 control grassland plots (matched by year) for each of the treatments. The data included estimates of species richness, cover of herbaceous and woody species, and density of woody species. We also recorded the aspect, slope (degrees), and elevation for each plot.

We estimated cover with the point-intercept method (Bonham 1989) and followed sampling protocols used by Channel Islands National Park (Halvorson et al. 1988). A 30-m-long tape was extended along a randomly selected compass bearing, and every 3 cm along the tape a thin metal rod was vertically lowered and the species of plant which it intercepted was recorded. The height of the tallest species intercepted by the point was also recorded. We made a list

Table 1. Sizes and timing of prescribed burns for three treatments and one control area in grasslands on the southwest side of Santa Cruz Island, California.

Area	Size (Ha)	Burn Date
Control	160	Unburned
Poso	340	Nov-93
Alegria	270	Dec-94
Sauces	490	Nov-95

of all species occurring in a 2-m-wide belt (one meter on either side of the tape) along the tape, and counted the number of shrubs and trees rooted within the 2-m-wide belt. Shrubs were recorded if they were more than half rooted within the belt, and each species was recorded as either a seedling (no lignification of the main stem) or adult.

Vegetation species were grouped into eight different guilds (Table 2), and we calculated four different estimates of abundance for each guild. These included absolute and relative percent cover, and the mean number and percentage of species/plot. We did not analyze the mean number and percentage of species/plot for native annual grass and alien perennial forbs because there were too few species for a meaningful test (n=3 and 2, respectively).

We calculated three indices of alpha diversity (local or within plot diversity) for burned and unburned areas using the program BIODIV (Baev and Penev 1995). Species richness (S) was measured as the presence of all species within the 30 x 2 m belt. Species diversity using abundance estimates (% absolute cover) was calculated with Hills N2 (N2), while species evenness was estimated using Molinari's index (E). We selected these indices based on their biological interpretability and recommendations made by Magurran (1988) and Alatalo (1981).

We estimated beta diversity (differential diversity between plots, habitats, or treatments) with Whittaker's beta, calculated as gamma diversity (total species within a treatment condition/within plot diversity S) (Shmida and Wilson 1985). Gamma diversity for each of the six treatment and control conditions was estimated as the total number of species summed across the preburn and three postburn seasons.

We used canonical correspondence analysis (CANOCO) (ter Braak 1995) to determine the influence of various environmental variables on species composition in the different treatment conditions. Variables used to test against the ordination scores included the percent bare ground and litter, slope (degrees), aspect (calculated as degrees from true north), elevation, and whether a plot was burned or not. We broke the analyses into four separate years: preburn and each of the three postburn years. Because rainfall varied between years we included each year as a covariate in the ordination, thereby adjusting the scores and holding the effect of precipitation constant. All species were included in the analysis, but we downweighted rare ones (ter Braak 1995). Monte Carlo simulation tests were used to test for the significance of the ordination scores for the first canonical axis and the entire ordination (ter Braak 1995).

Table 2. Vegetation guilds and the number of species/guild in grassland burn areas on the southwest side of Santa Cruz Island, California, 1993 to 1998.

Guild	Number of Species
Native Annual Forbs	51
Native Perennial Forbs	31
Native Annual Grass	3
Native Perennial Grass	5
Alien Annual Forbs	23
Alien Perennial Forbs	2
Alien Annual Grass	13
Shrubs**	12
Total	150

** There was only one species of alien shrub (*Marrubium vulgare*), so it was lumped with the others.

We performed analysis of variance with repeated measures (RmANOVA) to test whether the diversity indices, cover estimates, and number and percentage of species in each guild differed among burned condition (burned vs. unburned), the year a particular area was burned (burn area), and the number of years postburn (the repeated factor). The analyses were partitioned into between subjects and within subjects groups. Each measure of diversity and abundance was tested separately. We used scatterplots and normal probability plots to evaluate residuals from the univariate tests for determining whether the assumptions of normality, linearity, equal variances and no outliers were valid. To avoid problems with violations of the sphericity assumption of RmANOVA, we used the Huynh-Feldt epsilon adjustment of the univariate F-statistics and Wilks Lambda for the multivariate tests to determine the significance of the analyses. Cover values and percentage of species in each guild were arcsin transformed, and the mean number of species/plot in each guild was square root transformed. All statistical analyses were done using the GLM procedure of SYSTAT (Wilkinson 1990). Statistical tests were considered significant if $p < 0.05$, and marginally significant if $0.05 < p < 0.10$.

RESULTS

There was a significant between-subjects interaction among burned/unburned condition and burn area (F=4.55, df=2,54, p=0.01) for total species richness (S). There was no significant difference in S among burn conditions in Poso and Sauces, but S was significantly greater in burned than unburned plots for all postburn years in Alegria (Wilks Lambda=0.72, F=2.29, df=8,102, p=0.03). There was a significant within-subjects interaction between the year postburn and the burn area (F=5.13, df=6,162, p=0.000). Species richness decreased significantly in Sauces, increased significantly in Alegria, and did not change significantly in Poso (Figure 1A).

Species diversity (N2) varied significantly between the three burn areas for between-subjects cases (F=3.86, df=2,54, p=0.03). N2 was significantly lower in Sauces than in Poso or Alegria (Wilks Lambda=0.656, F=6.679, df=4,51, p=0.000), and significantly greater in Alegria than Poso (Wilks Lambda=0.562, F=9.923, df=4,51, p=0.000). There was a significant within-subjects interaction in burn condition, burn area and the year post burn (F=2.15, df=6,162, p=0.05). There was no significant difference in N2 between burned and unburned plots for preburn conditions in Poso

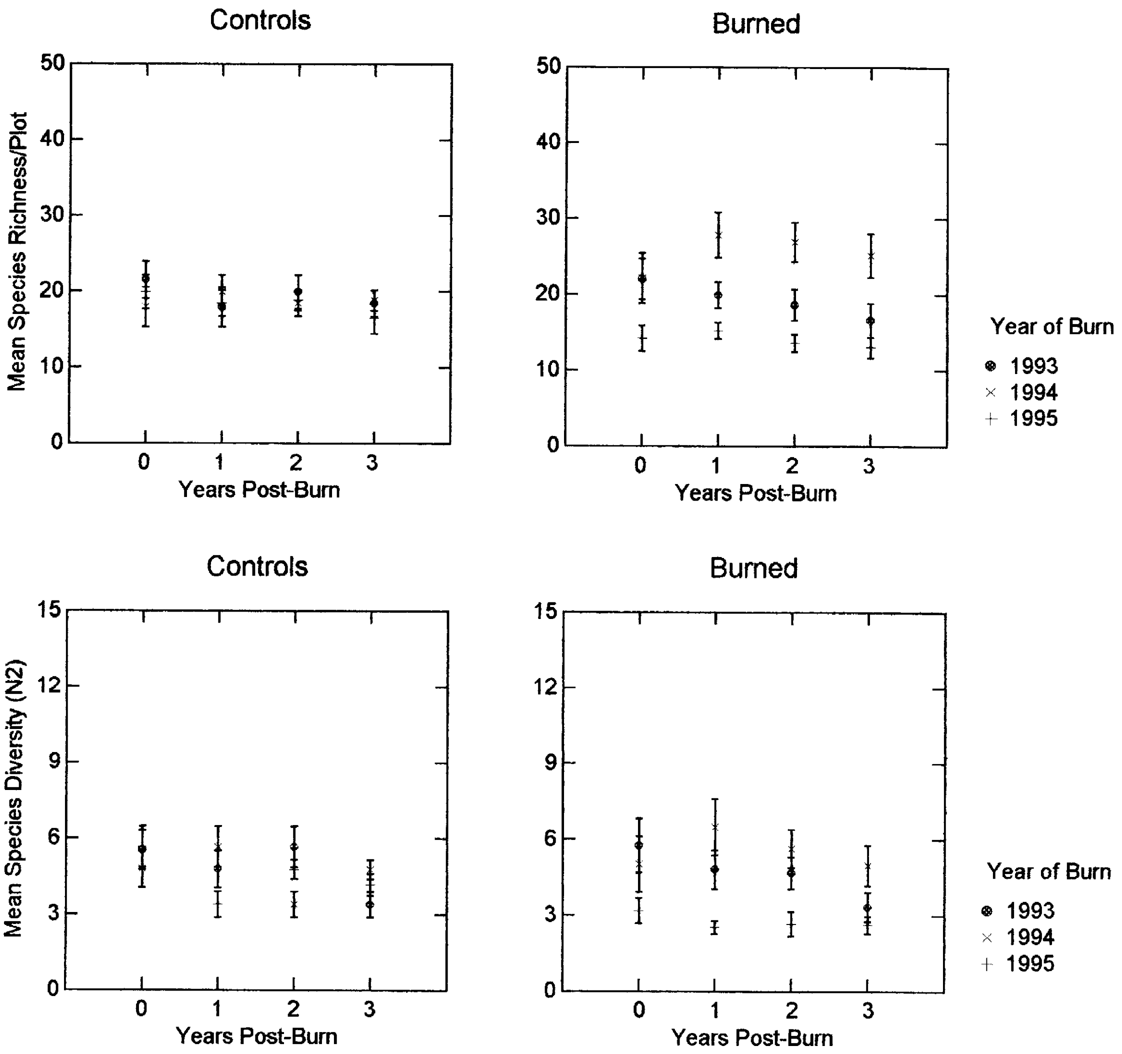

Figure 1A. Patterns of species richness and diversity in burned and unburned grasslands on Santa Cruz Island, California, 1993 to 1998.

and Alegria, but N2 was significantly lower in burned than unburned plots in Sauces. For postburn conditions, there was no significant difference in N2 between burned and unburned plots during any year in Poso. In Alegria, N2 was significantly greater in burned plots than unburned ones in the second year postburn. N2 was significantly lower in burned than unburned plots in Sauces during all years except the first postburn. There was an overall linear decrease in N2 between 1993 and 1998, regardless of burn condition or burn area (F=13.22, df=1,54, p=0.001) (Figure 1A).

There was a significant within-subjects interaction between burn area and the year postburn for beta diversity (F=3.984, df=6,162, p=0.003). Beta diversity showed a significant linear increase in Poso and a significant linear decrease in Alegria, and did not change significantly in Sauces (F=4.819, df=1,54, p=0.012) (Figure 1B). There were no significant between-subject differences in beta diversity among any of the burn condition or burn area combinations.

There was no significant difference in species evenness (E) among any of the burn condition or burn area combinations (F=0.79, df=3,162, p=0.50) (Figure 1B).

Three canonical axes could be interpreted in each of the four CANOCO ordinations. The three axes accounted for 76 to 83% of the variance between species composition and the environmental variables, and between 13 to 15% of the variability in the species abundance's (Table 3). All Monte Carlo tests for both the first canonical axis and the overall ordination were significant.

Species composition shifted dramatically as a result of burning, and this effect was most pronounced in the first year postburn (Table 3). In the preburn conditions, species composition was influenced most by the physical nature of the plots, specifically the aspect, elevation, and slope (Table 3). Before each burn, there was no distinct separation of plots or in species in different vegetation guilds (Figure 2A). In the first year postburn, species composition was

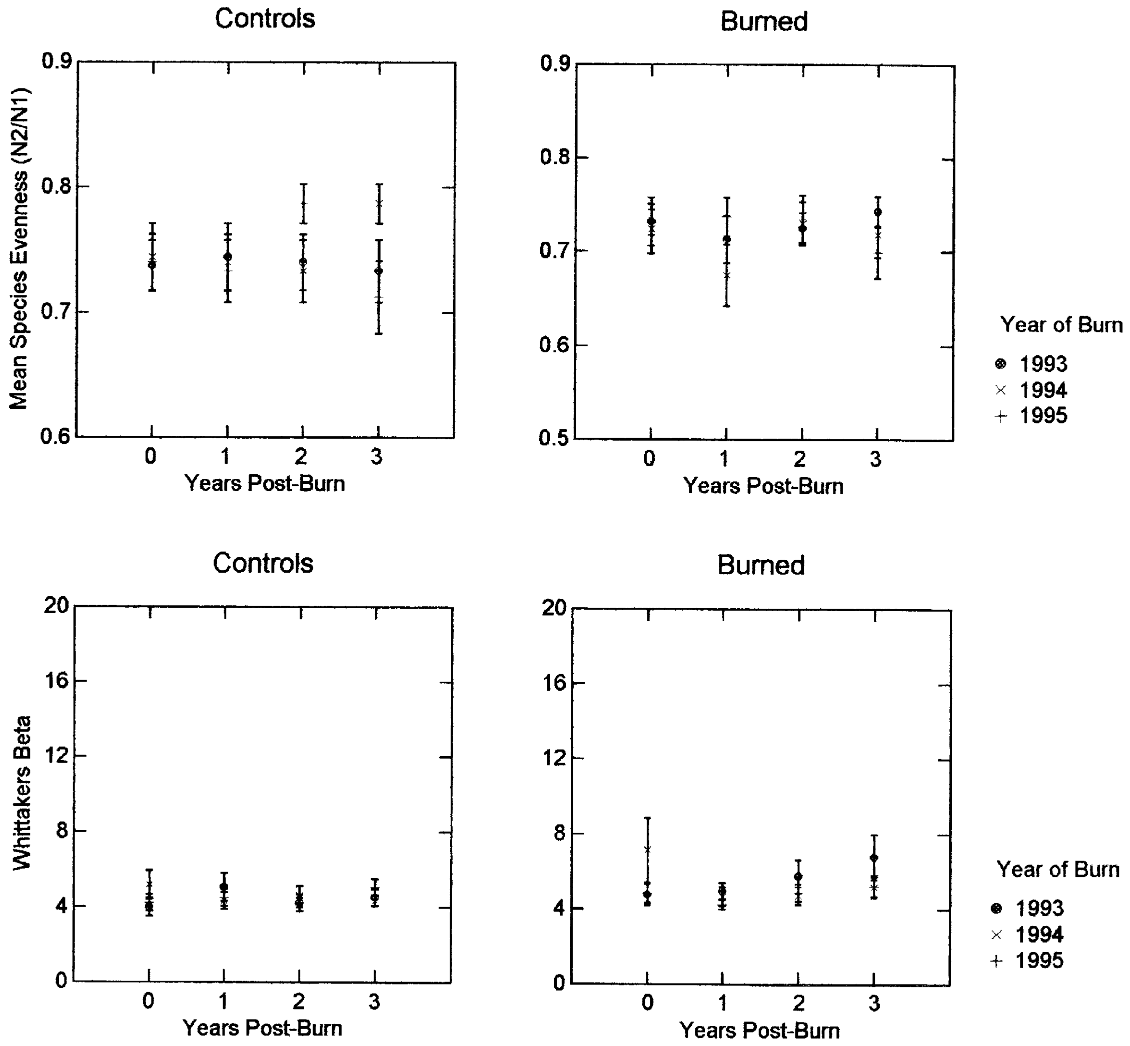

Figure 1B. Patterns of species evenness and beta diversity in burned and unburned grasslands on Santa Cruz Island, California, 1993 to 1998.

determined primarily by the burn condition of a plot. There was a distinct separation of burned and unburned plots, and there was a strong association in the distribution and abundance of most of the native forb species with burn plots (Figure 2B). This pattern continued into the second year postburn, although the association was not as strong as in the first year postburn. The correlation of burning with the first canonical axes dropped from 0.83 to 0.45, and species composition differences between burned and unburned plots were not as distinct (Figure 2C). By the third year postburn, the distinction in species composition had further weakened, and the correlation with species composition was more strongly influenced by the aspect of a plot than with burning (Table 3 and Figure 2D).

Alien grass and forb species were the dominant components of species richness and cover in all years and conditions (Figure 3). Over 60% of the species were comprised of members of these two groups. Alien annual grass comprised 69 to 71% of the relative cover in unburned areas and 63 to 70% in burned plots, while alien forbs comprised 14 to 16% in unburned areas and 13 to 21% in burned areas. Native forbs comprised 14 to 15% of the species in unburned plots and 19 to 25% in burned plots, while relative cover ranged from 1 to 3% in unburned plots and 3 to 6% in burned plots. The percent of native grass species ranged between 7 to 9% in unburned plots and 6 to 7% in unburned plots, while relative cover ranged from 8 to 11% in unburned plots and 6 to 10% in burned plots. Shrubs comprised 10% of the species in unburned plots and 5% in burned plots. The relative cover of shrubs ranged from 3 to 5% in unburned plots and 1.5 to 5% in burned plots.

Prior to burning, there was no significant difference between burned and unburned plots for the mean number and percentage of native annual forbs (F=0.51, df=2,54, p=0.60). Following burning there was a significantly greater number and percentage in burned than unburned areas

Table 3. Variable loadings and percent of variance accounted for three axis derived by canonical correspondence analysis of 150 plant species in burned and unburned grasslands on the southwest side of Santa Cruz Island, California, 1993 to 1998.

	Species Axis			Environmental Axis				Axes		
Variable	1	2	3	1	2	3	Summary	1	2	3
Preburn Conditions										
Bare Ground (%)	-0.018	0.652	0.159	-0.023	0.953	0.228				
Litter (%)	0.394	0.146	-0.093	0.489	0.213	-0.134	Eigen Value	0.120	0.069	0.060
Burned	0.217	0.086	-0.605	0.269	0.125	-0.866	*Species/Environment Correlation	0.806	0.685	0.698
Aspect	-0.629	0.093	-0.200	-0.781	0.136	-0.287	*Cumulative % Variance Species	7.2	11.4	15.0
Slope	-0.353	0.123	0.133	-0.438	0.180	0.190	Species/Environmental	39.8	62.7	82.7
Elevation	-0.437	-0.019	0.418	-0.542	-0.028	0.599				
1st Year Postburn										
Bare Ground (%)	0.393	-0.076	0.148	0.454	-0.094	0.267				
Litter (%)	0.031	0.536	0.263	0.036	0.667	0.475	Eigen Value	0.128	0.107	0.058
Burned	0.826	-0.139	0.035	0.954	-0.173	0.064	*Species/Environment Correlation	0.866	0.804	0.553
Aspect	-0.281	-0.516	0.297	-0.324	-0.642	0.537	*Cumulative % Variance Species	6.6	12.1	15.1
Slope	-0.277	-0.262	-0.119	-0.320	-0.326	-0.216	Species/Environmental	33.5	61.5	76.6
Elevation	-0.535	-0.110	0.120	-0.617	-0.137	0.217				
2nd Year Postburn										
Bare Ground (%)	0.152	-0.095	0.273	0.227	-0.128	0.419				
Litter (%)	0.097	-0.167	0.507	0.146	-0.226	0.778	Eigen Value	0.109	0.106	0.076
Burned	0.450	0.352	-0.271	0.679	0.478	-0.416	*Species/Environment Correlation	0.663	0.737	0.652
Aspect	0.225	-0.642	-0.137	0.339	-0.871	-0.210	*Cumulative % Variance Species	4.9	9.6	13.0
Slope	-0.275	-0.243	-0.055	-0.415	-0.329	-0.084	Species/Environmental	29.0	57.2	77.4
Elevation	-0.281	-0.346	0.131	-0.424	-0.469	0.201				
3rd Year Postburn										
Bare Ground (%)	0.237	0.350	0.120	0.337	0.571	0.219				
Litter (%)	0.023	0.136	0.348	0.033	0.222	0.636	Eigen Value	0.152	0.086	0.062
Burned	-0.319	0.384	-0.222	-0.454	0.626	-0.405	*Species/Environment Correlation	0.703	0.614	0.547
Aspect	0.646	-0.022	-0.161	0.919	-0.036	-0.295	*Cumulative % Variance Species	6.9	10.7	13.5
Slope	0.044	-0.062	-0.106	0.063	-0.101	-0.194	Species/Environmental	38.6	60.5	76.2
Elevation	0.139	-0.137	-0.107	0.197	-0.223	-0.195				

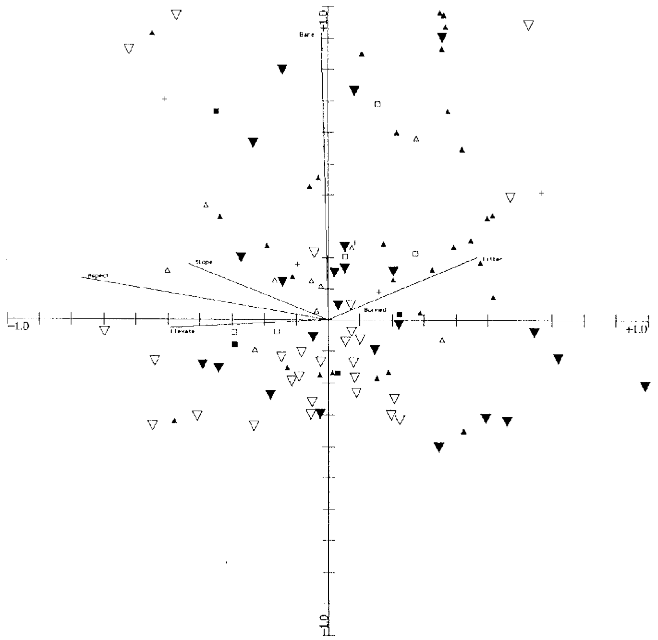

Figure 2A. Canonical Correspondence Analysis triplot of site and species scores for grassland plots on Santa Cruz Island, California. Symbols: large upside-down dark triangles=burned plots; large upside-down open triangles=unburned plots; small dark triangles=native forbs; small open triangles=alien forbs; small dark squares=native grass; small open squares=alien grass; crosses=shrubs. Data are for preburned conditions.

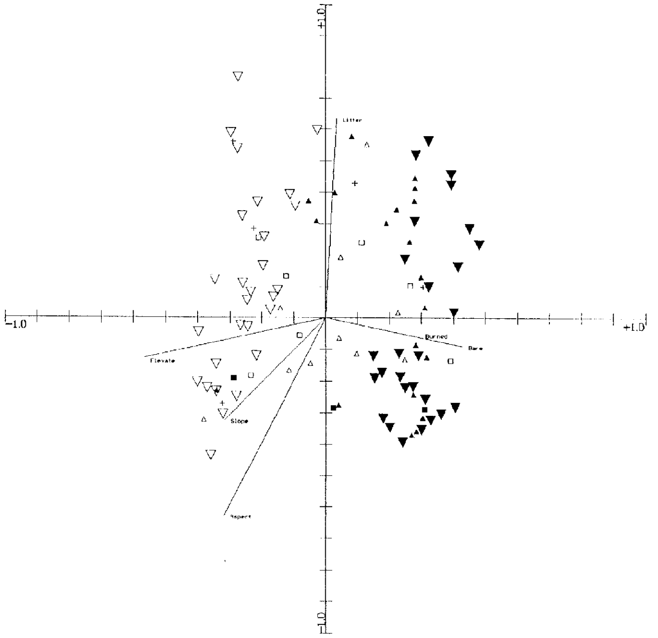

Figure 2B. Canonical Correspondence Analysis triplot of site and species scores for grassland plots on Santa Cruz Island, California. Symbols: large upside-down dark triangles=burned plots; large upside-down open triangles=unburned plots; small dark triangles=native forbs; small open triangles=alien forbs; small dark squares=native grass; small open squares=alien grass; crosses=shrubs. Data are for the first year postburn.

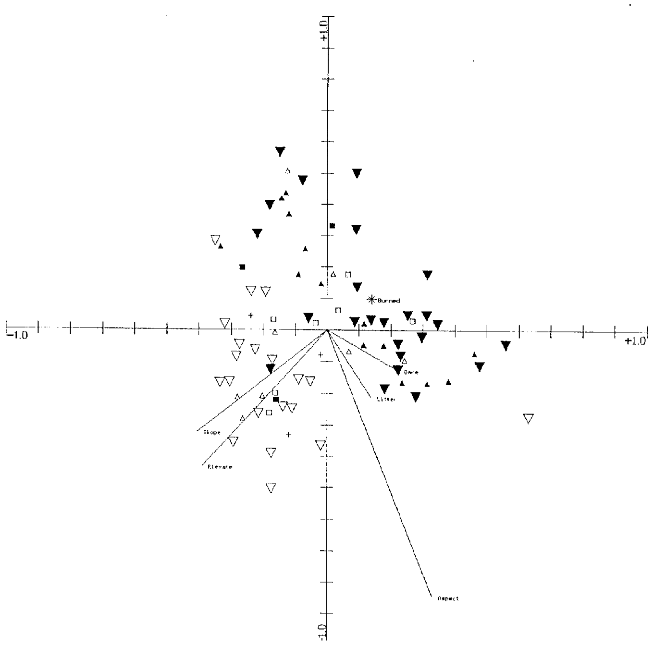

Figure 2C. Canonical Correspondence Analysis triplot of site and species scores for grassland plots on Santa Cruz Island, California. Symbols: large upside-down dark triangles=burned plots; large upside-down open triangles=unburned plots; small dark triangles=native forbs; small open triangles=alien forbs; small dark squares=native grass; small open squares=alien grass; crosses=shrubs. Data are for the second year postburn.

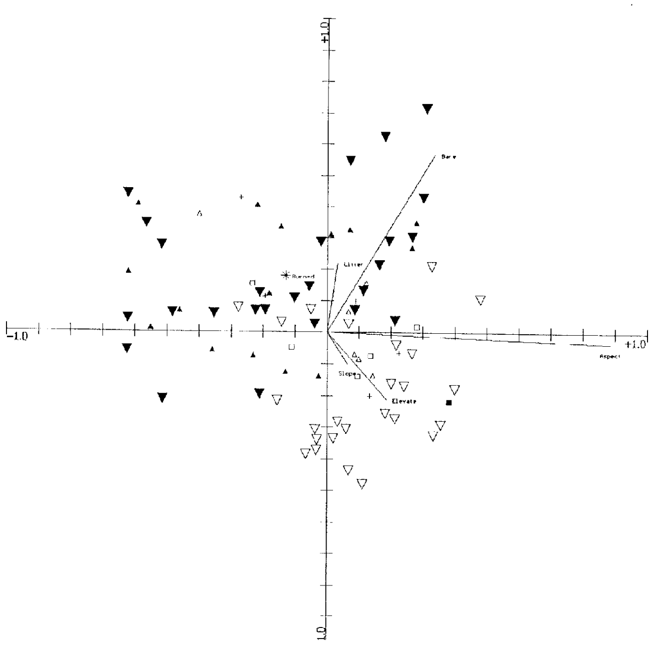

Figure 2D. Canonical Correspondence Analysis triplot of site and species scores for grassland plots on Santa Cruz Island, California. Symbols: large upside-down dark triangles=burned plots; large upside-down open triangles=unburned plots; small dark triangles=native forbs; small open triangles=alien forbs; small dark squares=native grass; small open squares=alien grass; crosses=shrubs. Data are for the third year postburn.

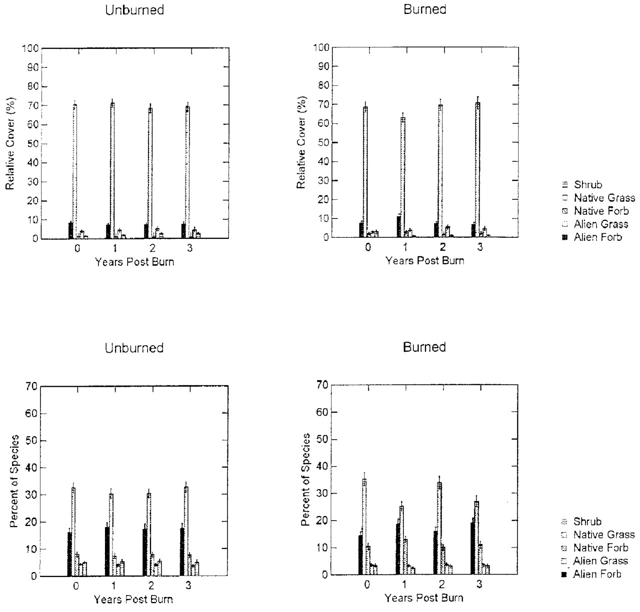

Figure 3. Relative percent cover and species composition for different vegetation classes in burned and unburned grasslands on Santa Cruz Island, California, 1993 to 1998.

(F=3.25, df=8,102, p=0.001). This pattern varied by the burn year and the year postburn (F=2.63, df=6,147, p=0.02), but the overall effect was a net increase, especially in the first year postburn. There was no significant difference between burned and unburned plots for absolute or relative cover in the preburn conditions, but cover was 3 to 4 times greater in burned than unburned areas in the first and third years postburn (Wilks Lambda=0.75, F=3.76, df=4,46, p=0.01).

The mean number of native perennial forb species differed significantly between burn condition and burn area for the between-subjects analysis (F=3.23, df=2,54, p=0.05). There was no significant difference between burned and unburned plots in Poso and Sauces, but there were significantly more in burned than unburned plots in Alegria (Wilks Lambda=0.82, F=2.75, df=4,51, p=0.04). The mean number of native perennial forb species varied significantly between the different burn years and the year post burn (F=2.40, df=6,162, p=0.03) for the within-subjects analysis. Consistent with the between-subjects analysis, there was no significant difference between burned and unburned plots in Poso and Sauces, but there was significantly more in burned than unburned plots in Alegria for all years. There was no significant change in the mean percentage of native perennial forb species in any condition.

There was a significant between-subjects interaction among burn condition and burn area for both absolute and relative cover of native perennial forbs (F=5.86, df=2,52, p=0.01), and also a significant within-subjects interaction between burn area and the year postburn for absolute and relative cover (F=2.75, df=6,159, p=0.02). There was no significant difference among the different conditions prior to burning, but after burning the burned plots in Alegria had significantly greater absolute and relative cover in all years than did unburned plots (Wilks Lambda=0.67, F=2.79, df=8,100, p=0.01).

The mean percent absolute and relative cover of native annual grass decreased significantly in all burn areas (F=8.41, df=3,93, p=0.001), but there was no difference in the pattern as a result of being burned or unburned (F=0.19, df=1,31, p=0.66). The mean percent absolute and relative cover of native perennial grass increased significantly in all burn areas and burn conditions (F=3.26, df=3,159, p=0.02).

There was a significant within-subjects interaction between burn condition, burn year, and the year postburn for the mean percentage of native perennial grass species (F=3.36, df=6,159, p=0.001). Their percentage increased significantly in burned plots in Poso and Sauces and in unburned plots in Alegria, but did not change significantly for burned plots in Alegria or unburned plots in Sauces. They initially decreased between preburn and the first year postburn in unburned plots in Poso, but then increased significantly in the last two postburn areas. In contrast, there was a significant between-subjects interaction between burn condition and burn area for the mean number of native grass species (F=3.45, df=23,54, p=0.04). This result is difficult to clearly interpret however, because the initial mean number of species was significantly higher in burned than unburned plots in Alegria, and in unburned than burned plots in Sauces (Wilks Lambda=0.72, F=2.28, df=8,102, p=0.03).

The mean number of alien annual forb species varied significantly among burn areas (F=3.07, df=2,54, p=0.05) but not by burn condition (F=0.29, df=1,54, p=0.59). There was a significant between-subjects interaction for the mean percent of alien annual forbs between burn condition and burn area (F=4.92, df=2,54, p=0.01); there was no significant difference between burned and unburned plots in Poso and Sauces, but the burned plots in Alegria had a significantly lower percentage than unburned plots. Absolute cover of alien annual forbs varied between years, burn area, and burned and unburned plots (F=4.03, df=6,162, p=0.000). There was no significant difference in the preburn plots in Poso and Alegria, but absolute cover was significantly greater in unburned plots in Sauces (F=5.36, df=1,54, p=0.001). In the first year postburn, burned plots had significantly greater absolute cover in Poso and Sauces, while burned plots in Poso and Alegria had significantly greater cover in the second year postburn. There was no significant difference in the third year postburn. The pattern for relative cover was the same as for absolute cover.

There was no significant difference in the percent absolute cover of alien perennial forbs in preburn plots (F=0.06, df=1,54, p=0.81), but unburned plots had significantly greater cover in the first year postburn (F=36.12, df=1,54, p=0.000). There was no significant difference in the second or third years postburn (F=2.37, df=1,54, p=0.13). The pattern for relative cover was the same as for absolute cover.

The mean number and percent of alien grass species varied among burned/unburned condition, burn area, and the postburn year (F=3.65, df=6,162, p=0.000). There was no significant difference among burned and unburned plots in any of the burn areas in the preburn years, or in any of the postburn years in Poso. In Alegria, there were significantly fewer species in unburned plots in the second year postburn, but fewer in burned plots in the third year postburn (Wilks Lambda=0.65, F=7.01, df=4,51, p=0.01). There were significantly more species in unburned plots in Sauces in the first and third years postburn (Wilks Lambda=0.80, F=3.19, df=4,51, p=0.02). The percent absolute and relative cover of alien grass varied among burned condition, burn area, and burn year (F=2.81, df=6,162, p=0.01). In Poso, there was no significant difference between burned and unburned plots in any of the burn years. There was no significant difference among burn conditions or burn areas for the preburn or third postburn years in Alegria and Sauces. Cover was significantly greater in unburned plots the first year postburn in Alegria, but was significantly greater in burned plots the second year postburn in both Alegria and Sauces areas.

The mean number and percent of shrub species varied among burned condition, burn area, and burn year (F=3.54, df=6,162, p=0.000). There were no significant differences among burned and unburned plots in any year for Poso and Alegria. In Sauces, there were significantly more species in unburned plots in the preburn and first two years postburn. The percent absolute and relative cover of shrubs varied among years between burned and unburned plots (F=12.04, df=6,126, p=0.000). There was significantly greater shrub cover in burned plots in the preburn years (F=4.35, df=1,42, p=0.04), but there was no significant difference between burned and unburned plots in the postburn years. The density of shrubs varied significantly between the different burn areas and years, but there was no significant difference in total shrub density or the density of seedlings or adults among burned and unburned plots.

DISCUSSION

From an ecological perspective, single fires appear to have only a temporary effect on structural aspects of grasslands on Santa Cruz Island. There were differences between burned and unburned conditions for some of the variables we measured, but in general, effects were dependent mainly on conditions intrinsic to the different areas. These differences were often inconsistent among years, treatments, and burn area as well. This outcome is similar to what Dyer et al. (1996) found at Jepson Prairie in northern California, where the regeneration of native bunch grass was as dependent on environmental variation as it was on burning or grazing treatments.

The effect of fire on diversity, structure, and composition was relatively brief and most pronounced in the first year postburn, and, to a lesser extent, the second year postburn. Species richness, alpha diversity, and beta diversity all varied after the burn, but in no distinct pattern; each area that was burned had a response different from the other areas. These differences appear to be related to site characteristics, although it is very possible that other factors such as rainfall patterns, weather during the fire, and fire intensity could be major influences as well.

Burning had little effect on the structure of the communities; alien grasses dominated the cover in all conditions, and although shrub cover in burned plots was reduced relative to preburn conditions, shrub density did not change in any significant way. Although it may seem contradictory for shrub density not to change while cover decreases, this is because the dominant shrub species occurring in the burned areas on Santa Cruz Island have the ability to resprout. So, although cover is reduced because leaves and stems are burned back, relatively few of the shrubs die and density remains about the same.

Some studies indicate postfire vegetation changes occur in a brief period of time (Holland 1986) and are characterized mainly by species already occurring within the burn area. Relative abundances can change, but the basic suite of species does not, a pattern called "autosuccessional" (Hane 1971). Our data support these hypotheses, and it is unlikely that diversity patterns would change in any systematic way under these conditions. Furthermore, because alien grasses produce rich seed banks, it is unlikely that a single fire would deplete these, and studies in grasslands throughout California have shown that alien grass continues to remain the most abundant group of plants after a burn (Parsons and Stohlgren 1989; Dyer and Rice 1997).

The most noticeable change brought on by fire was in species composition. Canonical correspondence analysis clearly indicated that burning has at least short-term effects on composition and can override site-specific factors that are the main determinants of composition in the absence of fire. The change in composition was not limited to individual species; some guilds, especially annual forbs, responded in consistent ways to the burns. Parsons and Stohlgren (1989) reported a similar pattern in grasslands in the foothills of the Sierra Nevada, and this pattern has been well-recognized for years in other Mediterranean climate communities (Trabaud 1994).

Fire ecologists have become increasingly aware that many factors interact to influence fire effects on species composition. These include the season a burn occurs, fire behavior (intensity, rate of spread, severity), the spatial and temporal scales associated with the fire regime, landscape level processes, and historical land use (Naveh 1994; Whelan 1995). In our study, topography was the primary determinant of species composition in unburned conditions, and it influenced species composition even in recently burned areas. The topographic influence was secondary to fire effects in the first two postburn years; however, by the third year after burning, fire effects were being masked by topographic characteristics. Different guilds showed different temporal patterns for species richness and abundance in the burned areas, but by the third year postburn virtually all guilds were essentially at the same relative levels as in unburned areas. Differences in annual rainfall likely had a weak effect on some guilds, and other factors for which we did not collect data (e.g., physical and chemical soil properties) undoubtedly did as well. Historically, all of the areas had different levels of grazing by feral sheep and livestock, which has had a notable influence on the relative amounts of bare ground between sites. Each of these factors will directly and indirectly influence fire effects by modifying fire behavior at local scales (intensity and duration), site scales (intensity, duration, extent, type), and landscape scales (intensity, duration, extent, type, seasonality, frequency). They also add complexity to evaluating fire effects, because different groups of species will show variable responses according to when, where and what types of data are being collected.

From a restoration perspective, single fires on Santa Cruz will have relatively little effect in enhancing grassland communities for native species. This appears to be characteristic of most grasslands in California where species composition has been drastically altered by grazing and the abundance of alien annual grasses (Dyer 1993; Dyer and Rice 1997). Although alien species continued to dominate burned areas in our study, the prescribed burns were an encouraging initial step in creating ecological conditions beneficial to native species. Most groups of native species either increased or remained the same in abundance, and alien species did not increase in abundance. However, it is clear it will be necessary to significantly modify species composition at both local and site scales before native species can begin to reach levels of abundance comparable to that of alien species (Dyer and Rice 1997).

Developing a prescribed burning regime that is beneficial to native species will take years of experimentation and evaluation at different scales. As Whelan (1995) points out, if conservation of biodiversity is the primary management goal, trying to determine and mimic a historical fire regime may be inappropriate. The ecosystem on Santa Cruz Island that the historic fire regime occurred in has been significantly altered, and it is unrealistic to expect the system to respond in the same way as it did in the past. It is more important to try and determine which components of a fire regime can be manipulated to benefit the most native species, and determine the range of environmental conditions that these can then be applied (Kilgore 1973).

Because our study only involved single burns done in the fall, making generalizations about fire effects on the islands would be premature. We encourage the use of small scale experiments to test differential effects of burning with variable seasons, frequency, and return interval, then applying these findings to relatively large areas where the influence of larger landscape level factors (topography, climate, environmental patchiness; fire duration, extent, intensity) on the management prescription can be evaluated. We also encourage incorporating different time scales to studies on fire in the California islands; individual projects should span several years, and evaluation of different burn studies should be done over several decades.

ACKNOWLEDGMENTS

We thank the California Department of Forestry and Bobby Ouellette from Alan Hancock College Fire Technology Program for providing crews and equipment to conduct the burns. Channel Islands National Park provided transportation to the island and logistical support. Lyndal Laughrin graciously made facilities and vehicles at the University of California Natural Reserve Station available for housing, meals, and transportation. Robin Wills, Jennifer Gibson, Oren Pollak, Tony Nelson, Mark Sanderson, Trish Smith, Ethan Aumack, Emily Hebard, Brian Kitzerow, Rick Young and Shirley Bailey of The Nature Conservancy helped in all aspects of planning, burning, support, and data collection. Numerous volunteers cut miles of fireline, helped collect data, or provided logistical support, especially Mark DiMaggio and Ken Ward with their students from Paso Robles High School; Joe Yuska and his students from Lewis and Clark College; and David Allen, Wendy Hatch, Rik Katzmaier, Shirley Imsand, Diane Lipkin, Tom Maxwell, Christopher and Mary-Louise Mueller, Marie Ofria, Tim Richards, Bill Turpin, and Jonathan Wheately. Robin Wills and two anonymous reviewers provided insightful editorial comments. Extra special thanks to John Conti, without whose quiet, patient and consistently high-quality efforts this project could not have been completed.

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