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# Response of a Native Perennial Grass Stand to Disturbance in California's Coast Range Grassland

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## Abstract

To assess the potential for enhancing an existing stand of native perennial grasses on a California Coast Range Grassland site, we experimentally manipulated the seasonal timing and presence of grazing for 3 years (1994 through 1996) and of autumn burning for 2 years (1994 and 1995) and measured species cover for 6 years (1993 through 1998). We subjected the species matrix to classification (TWINSPAN) and ordination (CCA) and tested the ordination site scores as well as diversity indices with linear mixed effects models. Four distinct plant community groups emerged from the classification. Two of these were dominated by annual grasses and two by perennial grasses. No treatment effects were observed on diversity. For composition, temporal and spatial random effects were important mixed effects model parameters, as was the fixed effect covariate, pre-treatment CCA site score, indicating the importance of random environmental variation and initial starting conditions. Incorporation of these random effects and initial condition terms made for more powerful tests of the fixed effects, grazing season, and burning. We found no significant burning

effects. Grazing removal imparted a shift in plant community from more annual-dominated toward more perennial-dominated vegetation. Individual perennial grass species responded differently according to genus and species. *Nassella* spp. increased gradually over time regardless of grazing treatment. *Nassella pulchra* (purple needlegrass) increase was greatest under spring grazing and *N. lepida* (foothill needlegrass) was greatest with grazing removal. *Danthonia californica* (California oatgrass) had little response over time under seasonal grazing treatments, but increased with grazing removal. Under relatively mesic weather conditions it appears that grazing removal from Coast Range Grasslands with existing native perennial grass populations can increase their cover. However if *N. pulchra* is the sole existing population, spring season-restricted grazing should be equally effective at enhancing cover of the native grass species.

**Key words:** burning, linear mixed effects models, live-stock grazing, native perennial grassland, ordination, restoration, TWINSPAN.

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## Introduction

Grazing effects on plants can be divided into effects of intensity and timing (Heady & Child 1994). Grazing intensity is usually measured as stocking rate (animals per unit area) for a given period, while timing of grazing is typically manipulated on a seasonal basis, if at all. Historically changes in grazing intensity were thought to control vegetation dynamics in a more or less linear and reversible fashion (Clements 1936; Dyksterhuis 1949; Ellison 1960). Species composition and productivity could be manipulated directly under this model, which continues to be useful in mesic systems (Martz et al. 1999; Paine et al. 1999; Carlassare & Karsten 2002) but has proven inadequate in arid and semiarid systems where environmental variability dominates vegetation dynamics (Westoby et al. 1989; Illius & O'Connor 1999; Oba et al. 2000; Sharp & Whittaker 2003).

Continuous, high-intensity livestock grazing began in the late eighteenth century in California and is believed to have contributed to alien plant dominance of grasslands (Burcham 1957). Grazing removal has been proposed as a way to enhance natives (Painter 1995), but with little success (Bartolome & Gemmill 1981). Grazing systems controlling both the timing and the amount of grazing have been proposed to both improve livestock production and protect plants (Heady et al. 1992).

Fire is used very effectively in native prairie restorations in the midwestern United States where shrubs and trees eventually encroach without disturbance (Heisler et al. 2003). However infrequent burning may lead to N pulses where plant litter has accumulated (Reever Morghan et al. 1999). This phenomenon has the potential to create an invasion window of opportunity for species with high N demands. Frequent use of fire has the potential to reduce soil N availability (Grogan et al. 2000), which should confer a competitive advantage to slower growing species with higher C:N ratios (Hobbs et al. 1991). Fire has been shown to affect composition in California plant communities as well (Hervey 1949; Parsons & Stohlgren 1989; Meyer & Schiffman 1999; Keeley 2002; Harrison et al. 2003). The most prevalent native grass, *Nassella pulchra* (purple needlegrass), responded favorably to burning in

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Valley Grassland (Dyer et al. 1996), but other results indicated this was a short-term effect (Dyer & Rice 1997). Removal of grazing and addition of burning failed to consistently enhance native grasses at a Coastal Prairie site in central California (Hatch et al. 1999).

California's Mediterranean grasslands and savannas cover about 5.5 million hectares (Allen-Diaz et al. 1999). They include the annual-dominated Valley Grassland of the interior part of the state and the Coastal Prairie, which typically contains a greater proportion of perennial species than Valley Grassland (Heady 1977). Based on floristic classification and significant differences from the Coastal Prairie, a third type of subcommunity, Coast Range Grassland, has been proposed (Jackson & Bartolome 2002). The greater San Francisco Bay Area contains examples of all three major Californian grassland types, but much of the hilly eastern side of the Bay is Coast Range Grassland, a type with little research history. One study included Coast Range Grassland sites in its statewide examination of the effects of varying amounts of residual dry matter on plant productivity (Bartolome et al. 1980) and another examined the relationships among cattle grazing, rodents, and species diversity (Fehmi & Bartolome 2002). Much of the land in the Bay Area Region is used for livestock grazing, often as part of an effort to reduce fire hazard. A large fraction of this grazed land is in parks and watershed preserves in which protection and enhancement of native vegetation is an important management objective.

We designed an experiment to determine the effects of altering the grazing season, removing grazing, and introducing prescribed burning in the Coast Range Grassland on vegetation composition and diversity. Results should guide livestock grazing practices, evaluate the effectiveness of grazing and burning as restoration and enhancement methods, and demonstrate the potential for restoration in this California annual grassland subtype.

## Methods

### Study Site

The study site, an area known as Sather Canyon (37.933 N, -122.244 W), faces northwest on approximately 20% slopes and is located above the eastern shore of San Pablo Reservoir in Contra Costa County, California. The East Bay Municipal Utilities District leases the approximately 200-ha pasture for year-long, continuous cattle grazing, which was occasionally heavy before 1993. The soil on the site was mapped as a fine-loamy, mixed, mesic typic argixeroll (Los Gatos Loam) by the Soil Conservation Service (Welch 1977). This soil series is typical of N-facing slopes in the uplands of Contra Costa County.

The vegetation is typical of the California coastal grassland around eastern San Francisco Bay, dominated by annual grasses of Mediterranean origin with scattered stands of native perennial grasses that potentially could

be enhanced by management. This region had a 50-year mean total annual rainfall of 732 mm (SD = 267 mm), with considerable variation in the timing and amount. Significantly, the 6-year period preceding this study (1987–1992) had consistently low rainfall (mean = 534 mm/year, SD = 34 mm), while rainfall was generally high during the 6-year study period (mean = 884 mm/year, SD = 239 mm). The annual grasses and forbs germinate with fall rains, and most grow until the moisture is exhausted from the site in late spring (Chiariello 1989). The native perennial grasses remain green longer into summer, as do a few summer annual forbs. Typically soil moisture is not a limiting factor for plant growth between November and May.

### Treatments and Data Collection

This experiment began in spring 1993 with the construction of permanent fences on the study site to create a split-plot design with 13 experimental units. The main experimental factor was livestock grazing, with three replicates of four treatment levels: (1) no grazing; (2) spring grazing; (3) summer grazing; and (4) continuous grazing. A fourth replication of summer grazing was also included. Grazing treatments other than continuous grazing were applied on a row of square paddocks, each 30.5 m on a side. One of the continuous grazing replicates was assigned to a paddock in the row, with the fencing partially removed. The other two continuous grazing replications were located randomly along the outside of the treatment fencing. Grazing treatments were assigned to paddocks at random and commenced in spring 1993 with the introduction of cattle into the pasture, starting the continuous grazing. The spring grazing treatment was applied in April 1993, 1994, and 1995 with several cows remaining in each paddock until a residual dry matter level of 750 kg/ha was achieved. The summer treatment was applied in the same manner in July 1993, 1994, and 1995. All treatments were suspended in 1996, hence the 1997 and 1998 sampling years reflect responses after one and two seasons of no livestock grazing, respectively.

The second experimental factor was autumn burning. Half of each paddock and a 15.2 m strip of the continuously grazed pasture were burned in November 1993 and 1994. Logistical constraints resulted in the burn being assigned to a single contiguous strip that included the S-side of the treated plots and the N-side of the contiguous grazing plots. The burning treatment was intended to follow germination of annual herbs, but the first rains of autumn 1993 were light and late, resulting in low germination rates. Because burn scheduling had been completed and the likelihood of suitable conditions after a germinating rain were rapidly decreasing, the burn was applied before significant annual germination. In 1994 the germination of annuals had commenced before burning.

Two randomly located points served as terminal points for parallel, permanent 5-m transects that were established within each experimental unit to estimate foliar cover by

species using the line-point method (Cook & Stubbendieck 1986). Each spring, before any grazing treatments had occurred, we recorded the initial foliar interception of 50 sharpened points that were lowered perpendicularly to the ground at 0.5-dm intervals.

#### Classification and Ordination

Transect-based, absolute cover data were subjected to TWINSpan (PC-Ord version 4, MjM Software Design, Glenden Beach, OR, U.S.A.) (McCune & Mefford 1999), an ordination-classification algorithm, to reduce the dimensionality of the dataset, define vegetation groupings, and assign transects to these groups for further examination. TWINSpan uses cover classes delimited according to cut-levels that specify class ranges, then uses each cover class  $\times$  species combination to create pseudospecies, e.g., *Bromus hordeaceus* (soft chess) 5–10% is considered a different taxon than *B. hordeaceus* 11–20%. Pseudospecies are then used to drive a divisive classification, each level of which is the result of bifurcating groups produced by previous divisions. The relative strength of a division, hence the resultant two groups, was denoted by an eigenvalue ( $\lambda$ ) showing increasing strength from 0.00 to 1.00 (Gauch 1982). Eigenvalues approximate the proportion of pseudospecies not common to each group, e.g.,  $\lambda = 1$  denotes two groups with no pseudospecies overlap (Jongman et al. 1995).

Pseudospecies cut-levels were set at >0–2, 3–5, 6–10, 11–20, 21–40, 41–60, 61–80, and >80% cover. This level achieved strong distinction between a perennial and annual dominance, as well as distinguishing some variability within each. Once obtained, these types were included as grouping variables for plotting in a canonical correspondence analysis (CCA, PC-Ord version 4) on the same species matrix with year as the single environmental variable. This approach separated each year along CCA ordination axis 1, effectively partitioning interannual variability and allowing subsequent CCA axes to address residual variability. The second and third ordination axes were not constrained by environmental factors, but were constrained to be orthogonal to CCA1 and each other and thus represented gradients in species space. Relationships between gradients and experimental factors could be inferred by modeling standardized site scores from which year effects had been removed.

#### Mixed Effects Modeling

We used linear mixed effects models (S-plus version 6.1, Insightful Corp., Seattle, WA, U.S.A.) to separate the fixed effects of management from the random effects of interannual variability at two spatial scales—plot and burn-within-plot. This ability to analyze repeated measures data makes mixed effects models more powerful than traditional ANOVA approaches (Piepho et al. 2003), which have strict assumptions about independence of observations that are usually not reasonable with ecological data. This

independence restriction would also render comparisons of our nonrandomized burn factor inappropriate with ANOVA. Finally mixed effects models allow for specification of heteroscedastic error structures and estimate parameters with maximum likelihood algorithms that are amenable to unbalanced designs and missing data (for a review see Piepho et al. 2003). We took advantage of all three of these characteristics.

One shortcoming of the commercially available software implementing mixed effects models is the lack of stable algorithms for analysis of non-normally distributed data, i.e., generalized linear mixed effects models. Our species-specific cover data contained many zeroes and were therefore non-normally distributed. Attempts to transform these data failed to normalize them. Therefore site scores from the second CCA axis (CCA2) served as a synthetic species composition response variable. Higher values were indicative of annual dominance and vice versa. Species-specific responses were assessed from barplots of medians and interquartile ranges. Diversity indices (species richness, species evenness, and Shannon index) also served as response variables. Both CCA2 and diversity indices were modeled as linear combinations of two fixed effects factors, grazing season (continuous, spring, summer, and none) and burning (burned, not burned), and a covariate, the 1993 pre-treatment values of each response variable (e.g., CCA2.93). Random effects from interannual variability were modeled at two spatial scales: the plot level ( $n = 13$ ) and the burn-within-plot level ( $n = 26$ ). The random effects structure was tested by sequentially removing each random effects term and comparing subsequent models and the saturated model with a likelihood ratio test (Pinheiro & Bates 2000).

Once the random effects structure was determined, likelihood ratio tests were used to compare alternative models that included parameter estimates for heteroscedasticity and serial autocorrelation within fixed effects groups. When necessary we modeled unequal variances among fixed factors by including separate variance parameter estimates at each treatment level ( $k$ ). This resulted in an additional complexity cost of  $k - 1$  degrees of freedom to a given model. We tested for and modeled temporal autocorrelation by employing an autoregressive correlation function (Pinheiro & Bates 2000). Briefly the autocorrelation function searches for the correlation of observations nearest each other in time and then assumes an exponential decay of correlation with each additional time step. If temporal correlation was present, this approach included an extra parameter in the final model, but accounted for the correlated structure at each time step. With temporal dependencies accounted for, this approach allows for greater power in testing fixed factors because observations from repeated measurements on the same experimental unit can be assumed to be independent. Akaike's information criterion (AIC) and Bayesian inference criterion (BIC) were used in conjunction with likelihood ratio tests for pairwise model comparison to determine the signifi-

cance of random effects and variance–covariance matrix parameters (Crawley 2002). Finally evidence for departures from normality were assessed with histograms.

With random effects terms specified and the variance–covariance matrix structure modeled, conditional  $F$ -tests were used to assess the significance ( $\alpha = 0.05$ ) of fixed effects factors (Pinheiro & Bates 2000). Nonsignificant factors were removed from the model, and the significance of  $t$  values associated with parameter estimates for each level of the resulting fixed factors was assessed ( $\alpha = 0.05$ ). The flow of our approach to data analysis is shown in Figure 1.

## Results

Four distinct plant community groups emerged from the TWINSpan classification. Two of these were dominated by annual grasses and two by perennial grasses (Fig. 2). Both annual groups were characterized by high cover of the annual grasses *Lolium multiflorum* (Italian ryegrass) and *Bromus hordeaceus* (soft chess) but were further delineated by either more annual grasses (Group 1) or annual forbs (Group 2) as subdominants. The perennial grass groups were dominated by the genus *Nassella* with *Nassella pulchra* typical of Group 3 and *N. lepida* (foothill needlegrass) typical of Group 4. Each of these perennial grass groups also had significant cover of the native perennial grass, *Danthonia californica* (California oatgrass). *Lolium multiflorum* (annual ryegrass) and *Plantago lanceolata* (ribwort) were abundant in these plots as well, comprising 20–30% of the total cover (Table 1).

Flow for analysis of composition data

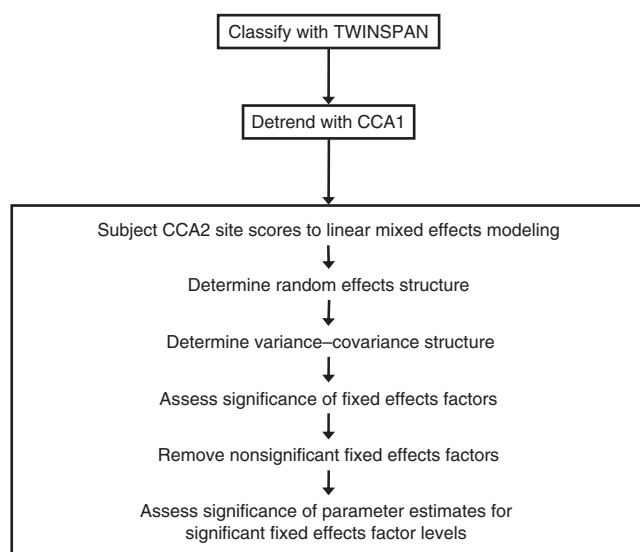


Figure 1. Flow of analysis for composition data. Two-way indicator species analysis (TWINSpan) was used to classify species matrix, which was also detrended for time by subjecting species matrix to canonical correspondence analysis. Lower box shows flow of linear mixed effects modeling.

CCA constrained an ordination of the species data so that the first axis extracted was the best linear combination of the environmental variables that we included; we included only year. As a result, plots were arrayed chronologically along the first CCA ordination axis (CCA1;  $\lambda = 0.14$ ), which was a linear function of the variable year (Fig. 3a). Subsequent ordination axes (CCA2 and CCA3) were not constrained by environmental data and had relatively high eigenvalues ( $\lambda = 0.45$  and  $\lambda = 0.37$ , respectively) indicating strong dispersion of the species data once interannual effects were separated (Fig. 3b).

A clear separation of the perennial and annual vegetation groups determined with TWINSpan was observed in the CCA2 versus CCA3 plot (Fig. 3b). Higher site scores on CCA2 corresponded with Groups 1 and 2, while lower scores indicated perennial Groups 3 and 4 where annuals were abundant, but perennial grasses dominated. Figure 3b shows that CCA3 distinguished *N. lepida*-dominated plots (positive) from *N. pulchra*-dominated (negative) plots.

While random effects due to year, plot, and burn were useful in partitioning error from the residual error term used to test fixed effects, no general effect of time was evident across our two levels of spatial blocking. Sequentially removing these terms significantly decreased the deviance explained by resulting models (compare Model A to Models B–E in Table 2) indicating that separate slope and intercept estimates for each plot  $\times$  burn combination were appropriate. Modeling of heteroscedastic errors significantly improved Model A (compare Model A to Model A1 in Table 2), but no evidence for serial autocorrelation was found for the CCA2 model (compare Model A to Model A2 in Table 2).

Conditional  $F$ -tests showed grazing season (graz) to be the only significant fixed effects factor (Table 3). Hence we dropped all other fixed factors from the model except the continuous variable CCA2.93, which was included to account for preexisting differences in composition. Parameter estimates for each grazing season treatment level were examined for significance with  $t$ -tests (Table 4). Grazing removal resulted in decreased CCA2 site scores (Fig. 4). Lower CCA2 site scores were indicative of a community comprised of more perennial grasses. Examination of medians and interquartile ranges for each perennial grass over time shows that each species responded somewhat differently to yearly environmental variability and grazing treatments (Fig. 5). Summer grazing caused a slight decline in *Danthonia* cover, while spring grazing had little effect on this taxon. All three perennial grasses responded favorably to the no-grazing treatment, while both *Nassella* species had positive post-treatment (i.e., grazing removal in 1996) responses. Spring grazing appeared to have a generally positive effect on *N. pulchra* cover, as it was increasing over time under this treatment.

No significant fixed effects were found for species richness, evenness, or the Shannon diversity index.

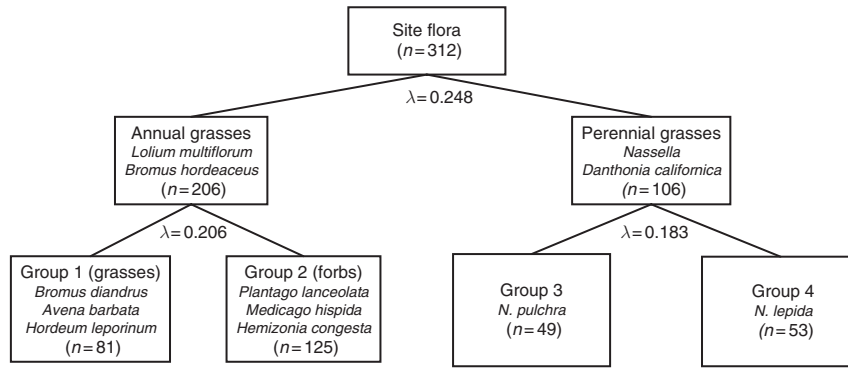


Figure 2. Dendrogram resulting from TWINSpan ordination-classification of transect-based cover data ( $n$  = number of transects per group). Groups were divided to create most dissimilar subsequent groups. Eigenvalues ( $\lambda$ ) are given as indication of goodness-of-split (where  $\lambda = 0.15$  was used as stopping rule) and can be loosely interpreted as proportion of taxa not overlapping between two groups (Jongman et al. 1995).

## Discussion

Disturbance effects on Californian grassland composition are site and time specific (George et al. 1992; Jackson & Bartolome 2002). This context dependency stems from high environmental variability at seasonal, annual, and decadal temporal scales (Talbot et al. 1939; Pitt & Heady 1978; Bartolome 1989) combined with a high degree of spatial heterogeneity in resource availability (Jackson et al. 1988; Gordon & Rice 1992; Hobbs & Mooney 1995; Stromberg & Griffin 1996; Reynolds et al. 1997). Grassland managers should work to match their geographic, floristic, and temporal setting to results from the growing catalog of field experiments examining management effects on community and population response under various environmental scenarios. This is similar to the opportunistic management of rangelands espoused by Westoby

et al. (1989) where managers are flexible enough to take advantage of transient situations when and where they emerge. The need for this type of approach in a restoration context was recently discussed by Bakker et al. (2003). In the northern Great Plains they showed that controlling the introduced perennial grass *Agropyron cristatum* in dry years and introducing native grasses in wet years afforded a greater likelihood for restoration success than trying to establish the natives year after year. A similar approach was espoused by Holmgren and Scheffer (2001), who suggested that El Niño-Southern Oscillation events be exploited for ecosystem recovery from overgrazing in regions where abnormally high levels of rainfall promote unusually high net primary productivity.

It is in this spirit that we report the results of seasonal disturbances on a Coast Range Grassland site during a

**Table 1.** Transect-based means (SE) of species cover (>1%), species richness, and percent bare ground by vegetation groups determined by TWINSpan classification.

Group 1		Group 2		Group 3		Group 4	
Number of transects	125	Number of transects	81	Number of transects	49	Number of transects	57
Species richness	8.4	Species richness	4.9	Species richness	8.1	Species richness	8.2
Bare ground (%)	5.2 (0.5)	Bare ground (%)	3.7 (0.6)	Bare ground (%)	4.8 (0.9)	Bare ground (%)	6.2 (1.1)
Taxon	Cover (%)	Taxon	Cover (%)	Taxon	Cover (%)	Taxon	Cover (%)
<i>Lolium multiflorum</i>	41.3 (1.3)	<i>Lolium multiflorum</i>	70.9 (1.8)	<i>Nassella pulchra</i>	27.4 (3.3)	<i>Nassella lepida</i>	26.9 (2.9)
<i>Bromus hordeaceus</i>	11.2 (0.9)	<i>Bromus hordeaceus</i>	7.5 (1)	<i>Danthonia californica</i>	6.7 (1.8)	<i>Danthonia californica</i>	11 (1.6)
<i>Plantago lanceolata</i>	9.7 (1.0)	<i>Bromus diandrus</i>	2.3 (0.8)	<i>Lolium multiflorum</i>	21.3 (1.8)	<i>Nassella pulchra</i>	4.9 (1.6)
<i>Medicago hispida</i>	4.7 (0.4)	<i>Avena barbata</i>	1.9 (0.4)	<i>Plantago lanceolata</i>	14.4 (1.3)	<i>Lolium multiflorum</i>	16.6 (1.6)
<i>Hemizonia congesta</i>	2.7 (0.4)	<i>Hordeum leporinum</i>	1.6 (0.4)	<i>Aira caryophylla</i>	5.6 (1.1)	<i>Plantago lanceolata</i>	12.1 (1.1)
<i>Aira caryophylla</i>	2.6 (0.3)	<i>Danthonia californica</i>	1.3 (0.4)	<i>Medicago hispida</i>	3.4 (0.7)	<i>Aira caryophylla</i>	3.2 (0.6)
<i>Hordeum hystris</i>	2.5 (0.6)	<i>Bromus madritensis</i>	1.2 (0.3)	<i>Bromus hordeaceus</i>	3.2 (0.4)	<i>Bromus hordeaceus</i>	3.1 (0.5)
<i>Nassella pulchra</i>	2.0 (0.7)	<i>Lupinus bicolor</i>	1.2 (0.5)	<i>Briza minor</i>	1.4 (0.5)	<i>Bromus madritensis</i>	2.9 (0.5)
<i>Danthonia californica</i>	2.0 (0.5)	<i>Plantago lanceolata</i>	1.2 (0.3)	<i>Avena barbata</i>	1.4 (0.5)	<i>Cynosurus echinatus</i>	2.4 (0.9)
<i>Geranium dissectum</i>	1.9 (0.2)			<i>Geranium dissectum</i>	1.1 (0.4)	<i>Medicago hispida</i>	1.1 (0.4)
<i>Lupinus bicolor</i>	1.5 (0.3)						
<i>Bromus madritensis</i>	1.2 (0.3)						
<i>Erodium botrys</i>	1.1 (0.2)						
<i>Hypochaeris glabra</i>	1.0 (0.3)						

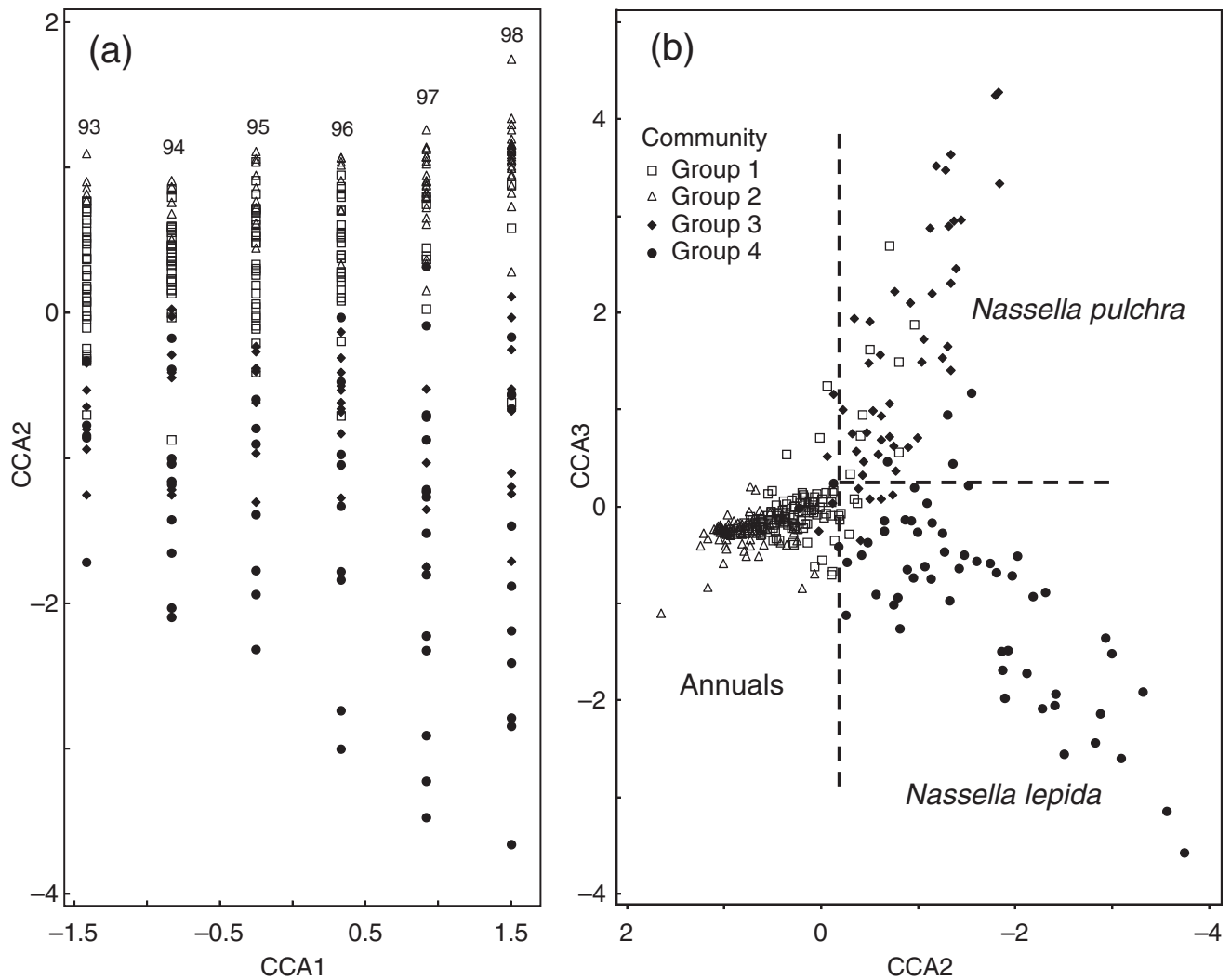


Figure 3. Canonical correspondence analysis (CCA) ordination results showing axis 1 versus axis 2 (a) and axis 2 versus axis 3 (b). Symbols vary by TWINSpan-generated vegetation groups. CCA axis 1 is a linear combination of the variable year (indicated above data). Lower scores on CCA axis 2 indicate perennial grass groupings.

relatively wet period (the last 4 of 5 study years received higher-than-average rainfall) following a 6-year drought. At the same time, all stakeholders in California grasslands should embrace the idea that very general models and inferences about the response of Mediterranean-type grasslands such as these will infrequently match the spatial and temporal scale at which management decisions are made. Responding to resource heterogeneity in time and space are a diverse suite of exotic annuals and native perennials that display idiosyncratic responses to management and weather at the community and species level (Evans & Young 1989). Management goals, which may range from diversity maintenance (Collins et al. 1998; Meyer & Schiffman 1999) to encouraging certain functional or taxonomic groups (sensu Menke 1992), must be informed by local understanding of environmental variables as well as historical and current floristic patterns. For example if perennial grasses are not present at a

site, grazing removal will not increase their abundance (Keeley 2001). Determining whether critical initial abundances exist and quantifying what they might be will require more research at many sites under many conditions.

Where perennial grasses were present at the onset of our study, grazing removal tended to increase cover. However over successive years cover increased in a similar fashion under both spring and summer grazing for both *Nassella* species, but not *Danthonia*. This follows from the work of Dyer and Rice (1997) in Valley Grassland showing that *Nassella pulchra* abundance increased only when released from diffuse competition with neighboring annual grasses and forbs. The shift in plot-level composition, as indexed by CCA2, was observed only where grazing was removed over the entire study period. These community-level results mirrored the *Danthonia californica* response to grazing treatments.

**Table 2.** Comparison of linear mixed effects models predicting CCA2 site scores as a function of 1993 CCA2 site score.

Model	Structure	Linear Combination	df	logLik	AIC	BIC	Model Comparison	p Value
<i>Random effects</i>								
Model A	Year × burn-within-plot	$CCA2 = \beta_0 + \beta_1 X + b_{plot} + b_{plot} X + b_{burn,plot} + b_{burn,plot} X$	23	-47.61	141.21	204.14	Model A versus Model B	0.001
Model B	Year × plot	$CCA2 = \beta_0 + \beta_1 X + b_{plot} + b_{plot} X$	20	-58.73	157.46	212.18	Model A versus Model C	<0.001
Model C	Year × burn	$CCA2 = \beta_0 + \beta_1 X + b_{burn} + b_{burn} X$	20	-70.79	181.59	236.32	Model A versus Model D	<0.001
Model D	Burn-within-plot	$CCA2 = \beta_0 + \beta_1 X + b_{plot} + b_{burn,plot}$	19	-64.69	167.38	219.37	Model A versus Model E	<0.001
Model E	None	$CCA2 = \beta_0 + \beta_1 X$	17	-70.79	175.59	222.11	Model A versus Model E	<0.001
<i>Variance-covariance matrix</i>								
Model A1	Unequal variances-zero covariance		30	-35.38	130.76	212.85	Model A versus Model A1	0.001
Model A2	Unequal variances-autoregressive correlation		31	-34.39	130.78	215.61	Model A1 versus Model A2	0.160

Random effects and variance-covariance structures were tested with a likelihood ratio test ( $\alpha = 0.05$ ). Degrees of freedom (df) = number of parameters estimated. Maximizing log likelihood (logLik) is accomplished by minimizing residual deviance of model. Akaike's information criterion (AIC =  $-2\logLik + 2n_{par}$ ) and Bayesian information criterion (BIC =  $-2\logLik + n_{par} \times \log(N)$ ), where  $n_{par}$  = number of parameters and  $N$  = number of observations) decrease as functions of residual deviance and the total number of parameters estimated; AIC is more sensitive to deviance reduction and BIC to parsimony. CCA, canonical correspondence analysis.

Responses of *D. californica* and *Nassella* spp. to fire and grazing regimes during drier periods may produce alternate results. The relative paucity of perennial grasses in Coast Range Grasslands (Huenneke 1989), even where livestock grazing has been excluded for decades, leads us to believe that the influence of multiple year to decadal rainfall patterns overrides grazing effects, though grazing's effects may be apparent during wetter periods. Merenlender et al. (2001) showed long-term variability of perennial grass density at a northern California site on permanently marked, ungrazed stands that were measured in 1958, 1979, 1991, and 2000. Over 50% of the initial *N. pulchra* stand density (approximately 2 plants/m) was lost from 1958 to 1979. Original levels returned by 1991, only to be reduced again by the 2000 sampling date. Annual grasses are known to be competitively superior to *N. pulchra* when water is the limiting resource (Jackson & Roy 1986) and have been shown to reduce *N. pulchra* abundance (Brown & Rice 2000). When water stress was eased by Hamilton et al. (1999), *N. pulchra* biomass and seed production responded similarly to when annual plant competition was suppressed indicating that under more consistent, higher moisture conditions the native perennial grass may increase abundance through aboveground growth as well as recruitment. Individual plants may endure drought periods by shunting resources below ground so that they are able to benefit from subsequent periods of higher rainfall. This would result in less aboveground biomass available for observation during drought years; hence greater relative cover of annual grasses and forbs would be recorded even though perennial grass individuals persisted below ground.

Bartolome and Gemmill (1981) rejected the notion that *N. pulchra* represents relictual dominance and hypothesized that it likely is a disturbance-adapted species that finds refuge in spaces where light is less limiting than belowground resources. Their hypotheses were largely confirmed by experimental findings of Dyer and Rice (1999). Dyer (2002) found that *N. pulchra* seed from grazed and/or burned individuals germinated and survived at higher rates than seed from undisturbed plants.

It should be noted that the site in this study was purposefully chosen to contain significant perennial bunchgrass cover. Perennial grasses should be more sensitive to grazing than annuals because with perennials the individuals sustaining defoliation and surviving are those that are actually available to be measured from year to year, while all the plant tissue of annuals are ephemeral. Indeed those sites maintaining significant perennial grass cover in another California grassland study, the mesic northernmost sites, showed the greatest sensitivity to disturbance treatments (Jackson & Bartolome 2002). Compositional change in our study was insignificant in annual-dominated plots, which varied little along either CCA2 or CCA3. This result aligns with other findings that annual grassland composition is generally unresponsive to changes in the timing of grazing (Heady 1961;



**Table 3.** Fixed effects ANOVA table for Model A1.

Term	num. df	denom. df	F Value	p Value
Intercept	1	104	3.91	0.051
CCA2.93	1	1	2.48	0.360
Graz	3	9	7.38	0.009
Burn	1	1	0.07	0.833
CCA2.93 × graz	3	1	1.35	0.548
CCA2.93 × burn	1	1	0.18	0.744
Graz × burn	3	1	1.27	0.560
CCA2.93 × graz × burn	3	1	0.36	0.806

CCA2.93 = 1993 pre-treatment CCA2 site scores. CCA, canonical correspondence analysis.

Bartolome 1984; Heady et al. 1992) and burning (see Keeley 2001 for review).

Fehmi and Bartolome (2003) conducted a spatial analysis of species distribution for the same Coast Range Grassland site discussed herein determining that the perennials appeared to be a simple addition to the annual plant matrix in which they were found, i.e., that they were not displacing populations of annuals. Examining Table 1 shows that by removing perennial grasses from Groups 3 and 4, the residual flora would strongly resemble Groups 1 and 2 except for the reduction in cover of the dominant annual, *Lolium multiflorum*. It will be interesting to monitor these plots through future drought–moisture cycles to determine whether perennials inversely covary with *L. multiflorum* and other annual dominants or are replaced by species not found during this wetter period.

It was surprising that we observed no management effects on diversity indices. Maranon and Bartolome (1994) found evidence for the well-known Intermediate Disturbance Hypothesis (Sousa 1979; Mackey & Currie 2000) in California annual grasslands occurring in Coast live oak (*Quercus agrifolia*) woodlands. However our experiment varied the timing of grazing and not grazing intensity, except where grazing was removed. We expected

**Table 4.** Linear mixed effects parameter estimates for Model A1.

Term	Estimate	SE	df	t Value	p Value
Intercept (continuous)	0.036	0.086	104	0.41	0.680
CCA2.93	1.097	0.095	12	11.57	<0.001
Spring	−0.084	0.112	9	−0.76	0.469
Summer	−0.098	0.145	9	−0.67	0.518
Not grazed	−0.581	0.130	9	−4.46	0.002

CCA2.93 = 1993 pre-treatment CCA2 site scores. CCA, canonical correspondence analysis.

species richness to decrease with grazing removal and to increase with burning; however this did not occur. Fehmi and Bartolome (2002) showed that a possible tradeoff between livestock and rodent herbivory exists in California annual grasslands. In their study rodents appeared to preferentially locate burrows, disturbing vegetation, in areas where livestock were excluded, i.e., high cover sites. Hence any response of diversity to livestock grazing regime changes may be canceled by rodent activity. Similar results were noted by Dyer and Rice (1997).

Variable effects of the timing of grazing on native perennial grass species in California support what restoration ecologists and preserve managers already know: simultaneously managing for a suite of native perennials is a terrific challenge. Burning had no apparent effect on perennial grass abundance. Likewise burning had no significant effect on plant diversity, which is contrary to findings in Valley Grasslands in the drier southern San Joaquin Valley (Meyer & Schiffman 1999). Differences in the vegetation subtype, burn timing and intensity, or grazing intensity interactions are all plausible explanations for these disparate findings. They serve to illustrate the difficulty in the development of general prescriptions for management. Finally variability in each of these perennial grasses increased substantially once all treatments had ceased in 1996. This variability indicates that the long-term effective-

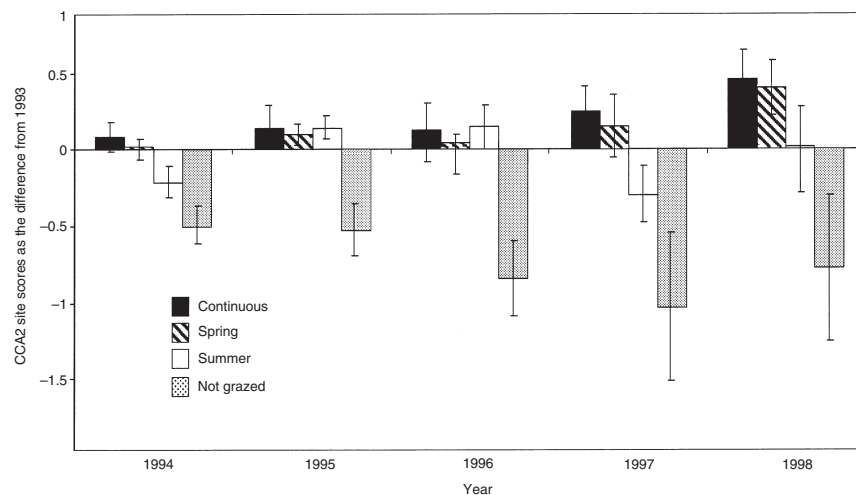


Figure 4. Mean ( $\pm$ SE) CCA2 site scores over years by grazing season treatment. CCA, canonical correspondence analysis.



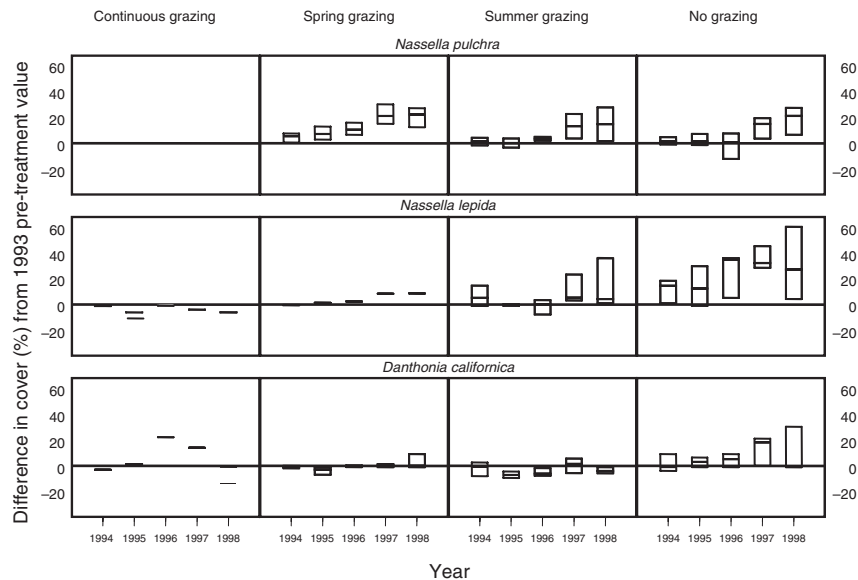


Figure 5. Boxplots for perennial grass responses relative to 1993 pre-treatment values. Lines within boxes are medians; boxes span the interquartile range (25–75%) of the data. *Nassella pulchra* was not present on continuous grazed plots.

ness of treatments is unpredictable; some plots increased desirable species cover dramatically and others decreased compared to any short-term (2–4 years) treatment effects that had been realized. The need for site- and time-specific information to guide such approaches cannot be overstated.

The most important characteristics for any restoration management scheme in Californian grasslands are flexibility and opportunism. Flexible schemes will adapt to changing conditions and improved understanding of system response to the environment and management. Opportunism implies that researchers and managers will embrace and learn from the nonequilibrium, variable nature of this dynamic ecosystem.

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