

SPRING-FED PLANT COMMUNITIES OF CALIFORNIA'S EAST BAY HILLS OAK WOODLANDS

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ABSTRACT

Sixty-eight spring ecosystems containing 207 plant species were sampled in 1991 and 1992 on the East Bay Hills of Alameda and Contra Costa Counties, California. Using TWINSPLAN, we identified and described four plant community types: 1) Ryegrass-Herbaceous, 2) Rush-Herbaceous, 3) Willow-Poison oak, and 4) California bay-Poison oak. Spring types were related to environmental gradients and a binary disturbance variable (livestock grazing presence/absence) using canonical correspondence analysis (CCA). Extraction of 2 CCA axes proved useful in relating spring types to productivity (using litter as proxy) and elevation gradients. A third CCA axis indicated that the presence or absence of grazing was somewhat helpful in discriminating among plant community types although gradients found with detrended correspondence analysis (DCA), which uses only the species matrix, were much stronger than could be generated by combining measured environmental and management factors (i.e., CCA). While community type, which was defined by taxonomic abundance, was apparently independent of grazing presence/absence, the grazing axis (CCA₃) was effective in dispersing willow size classes such that overstory willows scored higher on the ungrazed end and shrub willows scored higher on the grazed end of CCA₃. We conclude that grazing can affect vegetation structure of some spring-fed plant communities, but that composition is controlled by site variables.

Classification of California vegetation has a long and varied history. General descriptions of major vegetation types can be found in Jepson (1975), Munz and Keck (1973), as well as Ornduff (1974). More recently, *The Jepson Manual* (Hickman 1993) described major climatic and geographic zones in which plants can be found in California. Sawyer and Keeler-Wolf (1995) described California plant communities based on quantitative analysis of field plot data, or relied heavily on Holland's (1986) qualitative descriptions of communities if plot data were unavailable.

Many vegetation classification systems have been developed for specific purposes. For example, oak woodlands were described to subseries to provide baseline, quantitatively-based descriptive information for the Integrated Hardwood Range Management Program (Allen et al. 1989). Ferren et al. (1994) provided a detailed framework for classification of wetlands of the central and south coast of California for the Environmental Protection Agency. Gordon and White (1994), Fites (1993), Smith (1994) and other USDA Forest Service ecologists have intensively sampled plant community diversity on their forests to provide fundamental information for improving communication between diverse resource specialists as well as providing eco-

logical information on potential community responses to management.

The oak woodlands of California have been of particular interest to ecologists and managers over the past 15 years. Political awareness arose out of perceived threats to the oak woodland from urban development, wood cutting, lack of oak regeneration and recruitment, and livestock grazing (Muick and Bartolome 1987; Bolsinger 1988). In a political response, a research, extension, and management program was forged; the Integrated Hardwood Range Management Program (IHRMP) was developed to direct and fund research and extension activities in California's oak woodlands (Passof and Bartolome 1985). The IHRMP has supported a number of studies on oak ecology, oak woodland ecology and management, wildlife, invertebrates, regeneration and recently water quality (Swiecki and Bernhardt 1991; Allen-Diaz and Holzman 1993; Davis et al. 1995; Campbell and Allen-Diaz 1997; Allen-Diaz et al. 1998; Allen-Diaz and Jackson 2000).

A concern of many government water quality agencies and private conservation groups are livestock effects on wetland and riparian systems. Predicting the effects of livestock grazing on riparian areas such as spring-fed wetlands remains elusive (Clary 1995; Larsen et al. 1998; Belsky et al. 1999; Clary 1999; Rinne 1999; Allen-Diaz and Jackson 2000). These systems respond to grazing treatments

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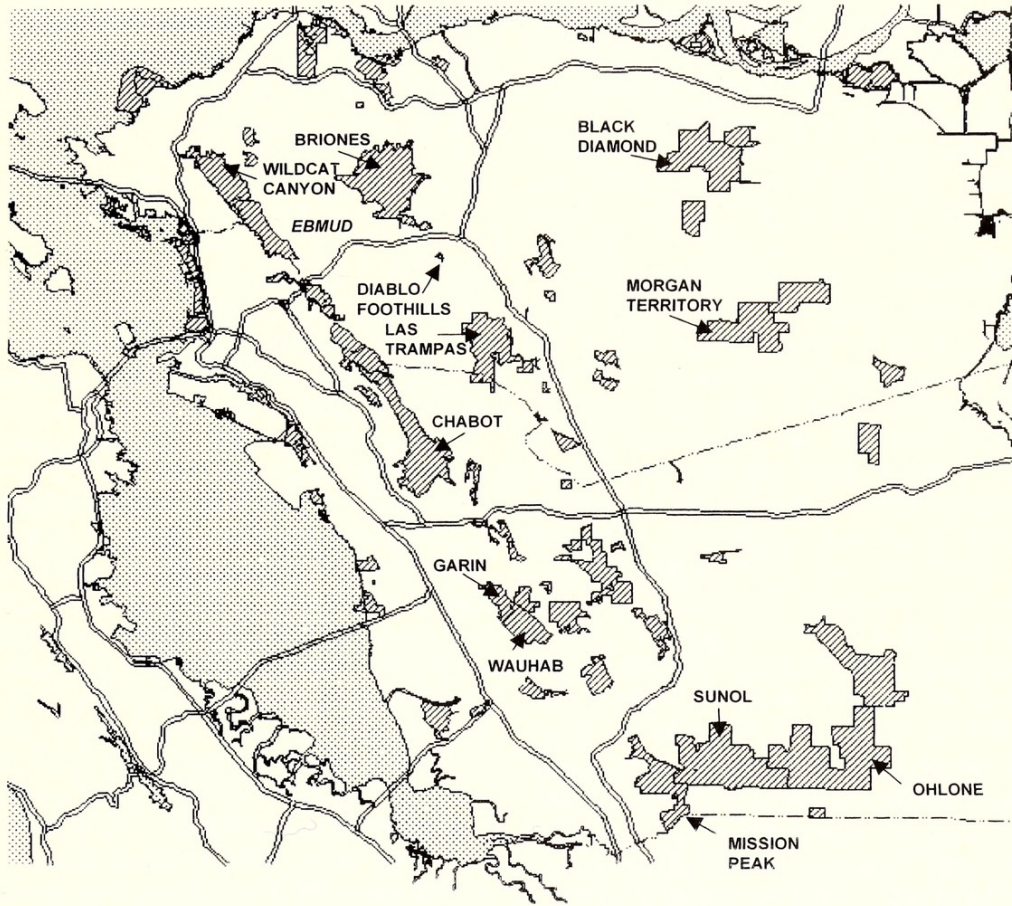


FIG. 1. East Bay Regional Parks and East Bay Municipal Utility District areas where springs were located.

in ways that do not always correspond with anecdotal and observational evidence (Kauffman and Krueger 1984). Disparity among results may lie in: 1) the confounding of grazing histories and other land-uses both past and present, 2) the application of grazing treatment levels that are not reflective of actual livestock use, 3) ambiguous or vague grazing system definitions, intensities, and seasons, 4) characteristics inherent to riparian ecosystems (i.e., non-equilibrium or chaotic dynamics), and/or 5) averaging of variability from site-specific responses. It follows that adequate description and understanding of riparian areas is lacking.

Nonetheless, management mandates abound. The 1987 renewal of the 1977 Clean Water Act amendment to the Federal Water Pollution Control Act of 1972 (PL 92-500; 33 U.S.C. s/s 1251 et seq.) shifted nonpoint-source pollution control emphasis from “direct threat to human health or safety” to “threat to ecosystems and habitat” (Sec 319). Revision of the Coastal Zone Management Act of 1992 (as amended by PL 92-583; 16 U.S.C. 1451 et seq.) required states to develop and implement nonpoint-source pollution programs and establish management measures for implementation. Moyle et al. (1996) contains appendices listing riparian protection guidelines and prescriptions on federal and private lands.

The East Bay Regional Park District (EBRPD) has recently conducted hearings to collect public

and expert input to guide future management on park landscapes. Hence, we sought coarse-scale patterns that might indicate whether community types at spring-fed ecosystems were influenced by the presence or absence of livestock grazing. Toward this end, we described and classified spring-fed plant community types on the hardwood rangelands of California’s East Bay Hills and then related these vegetation types to environmental and management factors. These results should inform future survey stratification and experimental design.

STUDY SITES

The East Bay Municipal Utility District (EBMUD) owns and manages approximately 11,330 ha in the East Bay (Fig. 1). EBMUD’s reservoirs store high-quality drinking water for approximately 1.2 million users. Domestic livestock grazing has been a significant component on these rangelands for at least 100 years. At the time of this study, cattle were managed on 7285 ha, with 22,000 AUM’s (animal unit months) grazed annually (EBMUD 1995).

The EBRPD manages 36,834 ha (20,457 ha in Alameda County; 16,377 ha in Contra Costa County) in 50 regional parks (EBRPD 1996). In 1992, about 15,785 ha were leased to grazing cattle for an authorized use of 24,000 AUM’s (EBRPD 1992). Ungrazed spring sites were determined by

TABLE 1. EAST BAY REGIONAL PARK DISTRICT AND EAST BAY MUNICIPAL UTILITY DISTRICT SAMPLING SITES. ¹ Number of sites.

Site	Grazed	Ungrazed	¹ Means of grazing exclusion
EBRPD			
Black Diamond	2	0	
Briones	7	0	
Chabot	0	1	fence
Diablo Foothills	1	0	
Garin	1	1	fence
Las Trampas	2	2	topography (2)
Mission Peak	3	2	fence (2)
Morgan Territory	6	1	fence
Ohlone	4	0	
Sunol	2	3	fence (2), topography (1)
Wauhab	2	0	
Wildcat Canyon	10	2	fence (1), topography (1)
EBMUD			
North	11	1	fence
South	4	0	
Totals	55	13	

assessing their physical accessibility (fences, shrub cover, topography) and evidence of livestock absence (no fecal material, untrampled soil, ungrazed vegetation). Specific dates of livestock exclusion were not available, but all fencing material had apparently aged substantially and exclusion by shrubs and topography would have existed for decades to millennia (or at least as long as the development of the spring itself).

The goals of the EBMUD and EBRPD livestock grazing programs are to manage livestock in order to maintain and enhance the health of the grassland ecosystem, remove fuels where fire poses a significant hazard, maintain a healthy agricultural economy where consistent with other district goals, protect and enhance water quality, and generate revenue (EBRPD 1992, EBMUD 1995).

METHODS

Data were collected March through June of 1991 and 1992 from 68 (55 grazed and 13 ungrazed) spring sites (Table 1). Sites were found by locating them on 7.5" quadrangle topographic maps. Sites were then visited and selected if vegetation indicated an active spring and no recent disturbance to develop the spring for livestock use was evident. Sampled sites included those maintaining old weir boxes (indicating past development) but exhibiting established vegetation, as well as springs that had apparently never been developed.

A sharp ecotone was present between spring vegetation and surrounding upland areas, which allowed for point-source designation along the upslope boundary, i.e., the point from which water flowed. Where weir boxes had been previously installed, the downslope side of the spring box or pond was considered the point-source.

Elevation, aspect, slope, slope position, and soil parameters were estimated for each site. Vegetation data were collected from two 10-m point-intercept transects (Bonham 1989) run parallel to streamflow and emanating from a randomly located point on either side of the spring head but confined to the "green zone" delineating spring vegetation (Fig. 2). Herbaceous plant species that were intercepted by a sharpened point lowered at 10 cm intervals along each transect were recorded for a total of 200 point-observations per site. A 5-m radius circular plot centered on the spring head was used to ocularly estimate relative cover of trees and shrubs. Bias and measurement error were minimized by ensuring that all plots in each year were estimated by a single individual (Elzinga et al. 1998). The difficulty of ocular estimation of cover increases with the number of taxa present (Elzinga et al. 1998),

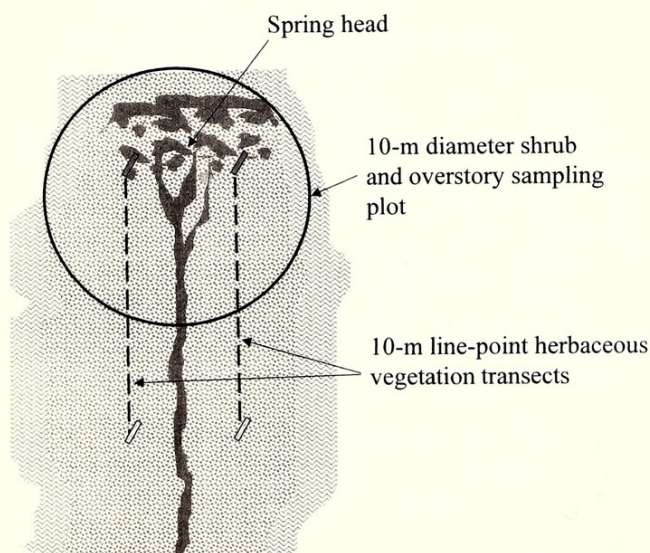


FIG. 2. Spring site sampling schematic.

however most of our plots were dominated by only two or three tree and/or shrub species. Fine-scale differences in these vegetation layers by species combinations were not instrumental in the subsequent classification. Unknown species were collected and keyed to species using Munz and Keck (1973) and then updated according to Hickman (1993).

We delineated plant communities by subjecting the combined herbaceous, shrub, and tree layer cover data to the classification software TWINSpan (PC-ORD version 4, Hill 1979; McCune and Mefford 1999). TWINSpan uses cover classes delimited according to cut-levels that specify class ranges. Default cut-levels were used resulting in absolute cover classes of >0 to 2%, 3 to 5%, 6 to 10%, 11 to 20%, and >20%. TWINSpan uses each cover class x species combination to create pseudospecies, e.g., *Bromus hordeaceus* L. 6–10% 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 2 groups, was denoted by an eigenvalue (λ) showing increasing strength from 0.00 to 1.00 (Gauch 1982). Eigenvalues approximate the percentage of pseudospecies not common to each group, so, $\lambda = 1$ denotes 2 groups with no pseudospecies overlap (Jongman et al. 1995). Eigenvalues provide an objective criterion for determining the merit of each division, although, the λ at which further splits are ignored (the critical λ) is a subjective choice dependent on the research question. We sought a relatively broad scale classification so $\lambda = 0.30$ was used as our critical λ .

Canonical correspondence analysis (CCA, PC-ORD version 4, McCune and Mefford 1999; Ter Braak 1986; Ter Braak 1987) was employed to relate environmental and management factors to the vegetative groupings determined with TWINSpan. CCA finds the linear combination of these factors that maximizes species dispersion along an ordination or canonical axis. As with TWINSpan, the strength of this dispersion is indicated by an eigenvalue (λ). The correlation of environmental variables to canonical axes was assessed by examining intraset correlations (Palmer 1993). The correlation matrix of environmental variables indicated no multicollinearity problems. Monte Carlo tests of significance were run with 99 iterations for each canonical axis.

Three of the 68 sites were eliminated from the CCA analysis because they contained missing values. Eight environmental variables were entered into the CCA. The variable ASPECT was created by taking the absolute value of 180 minus the azimuth reading resulting in values ranging from 0 for south and 180 for north (*sensu* Stohlgren et al. 2000). Only 3 textural classes were evident at these sites: loam, clay loam, and clay. Hence, binary

dummy variables were created as LOAM or CLAY-LOAM with all other sites classified as CLAY. The presence or absence of livestock grazing was also coded as a binary dummy variable (GRAZED). The remaining variables were continuous: ELEVATION (m), SLOPE (%), LITTER (% cover of all dead organic matter), and BARE (% cover of bare ground).

Finally, DCA (PC-ORD version 4, McCune and Mefford 1999) was performed on the species matrix to assess the ability of CCA-generated ordination axes to depict important underlying gradients. DCA extracts ordination axes from the species matrix as does CCA, but DCA ordination is not constrained by specified environmental variables. DCA simply maximizes species dispersion using a 2-way weighted averaging algorithm (Jongman et al. 1995). Hence, DCA provides some indication of the total amount of dispersion or variability in a species matrix, while CCA shows how a combination of environmental or management variables can emulate this dispersion. If DCA and CCA generate gradients of similar magnitude (i.e., $\lambda_{DCA} \approx \lambda_{CCA}$) we would conclude that the environmental variables provide a *well-specified* model of gradients in the species matrix. Conversely, an *under-specified* CCA model is one where the combination of environmental and management variables do not approximate gradients generated from the species matrix alone (i.e., $\lambda_{DCA} \gg \lambda_{CCA}$). In practice, λ_{DCA} will always be greater than λ_{CCA} , so comparisons must remain qualitative and used in an exploratory manner as we have done here. A distinction must be made between using these ordination techniques for testing hypotheses (i.e., where manipulations of treatment variables are made) and for exploring structure or pattern in a dataset. A rigorous experimental design would include *a priori* grazing contrasts that were randomly assigned to each site. In this case, a balanced design where equal numbers of grazed and ungrazed sites were sampled would be ideal. However, ours was a heuristic use of ordination to search for possible relationships between environmental and management variables and community types and to examine how sites were distributed along these gradients. Our unbalanced design (more grazed than ungrazed sites) does not affect this technique because it was not an experimental design, but an exploratory analysis.

RESULTS

A total of 207 plant species were found on the springs, including 16 trees and 4 shrubs. Four oak species were found at the springs, coast live oak (*Quercus agrifolia* Nee), valley oak (*Q. lobata* Nee), blue oak (*Q. douglasii* Hook. & Arn.), and interior live oak (*Q. wislizeni* A. DC.). In addition, willow (*Salix* spp.) and California bay (*Umbellularia californica* [Hook. & Arn.] Nutt.), and sometimes alder (*Alnus rhombifolia* Nutt.), California

TABLE 3. RYEGRASS-HERBACEOUS TYPE DESCRIPTIVE STATISTICS. Constancy equals the number of species occurrences/total number of plots; cover equals the mean cover (%) of a species for a given type; and range equals the range of cover values (T = trace or <1%).

		Con- stancy	Cover	Range
Characteristic plant taxa				
<i>Lolium multiflorum</i> Lam.	ryegrass	94	12	T-44
<i>Juncus bufonius</i> L.	toad rush	69	4	T-22
<i>Rorippa nasturium-aquatica</i> (L.) Hayek	watercress	67	6	T-39
<i>Polypogon monspeliensis</i> (L.) Desf.	rabbitfoot grass	44	3	T-33
<i>Bromus diandrus</i> Roth	ripgut brome	44	1	T-8
<i>Juncus xiphioides</i> E. Meyer	iris-leaved rush	39	4	T-31
<i>Bromus hordeaceus</i> L.	soft chess	36	1	T-7
<i>Mimulus guttatus</i> DC.	common monkeyflower	31	2	T-29
<i>Geranium molle</i> L.	common geranium	28	1	T-4
<i>Hordeum marinum</i> Hudson	Mediterranean barley	28	1	T-10
<i>Juncus effusus</i> L.	bog rush	28	10	1-29
moss	moss	28	T	T-1
Biotic environment				
Total Vegetative Cover (%)	71 (35-100)			
Tree Cover (%)	49 (1-100) n = 14			
Shrub Cover (%)	13 (1-50) n = 13			
Grass Cover (%)	43 (1-85) n = 36			
Forb Cover (%)	13 (1-65) n = 36			
Abiotic environment				
Elevation (m)	376 (128-817)			
Slope (%)	21 (0-65)			
Aspect	SW primarily			
Position	Mid-slope, upper/lower slopes, draws			
Bare (%)	25 (1-62) n = 36			
Rock (%)	5 (1-21) n = 20			
Soil Series	Los Osos, various			
Texture	Clay loam, sandy clay loam, loam			
Coarse Fragments (%)	22 (1-60) n = 14			
Rootability	Hard & massive, hard & fractured			
Soil Drainage	Somewhat-poorly to poorly drained			

buckeye (*Aesculus californica* [Spach] Nutt.), or big-leaf maple (*Acer macrophyllum* Pursh), were common on springs with a tree overstory. Willows were identified to genus because of poor catkin years.

Spring herbaceous species were diverse and were significant in identifying spring types. No rare, threatened or endangered species were identified in the spring samples.

Spring plant communities. We identified 4 plant community types for the East Bay Hills oak woodlands (Table 2). The initial split by TWINSpan divided the tree-dominated types from the herbaceous-dominated plots ($\lambda = 0.608$). The herbaceous types were distinguished from one another based on the amount of sedges (*Carex* spp.), rushes (*Juncus* spp.), and horsetail (*Equisetum arvense* L.) present, all indicative of wetter sites ($\lambda = 0.418$). Two tree-dominated types were distinguished when TWINSpan separated California bay from willow sites ($\lambda = 0.531$).

Ryegrass-herbaceous type.—The Ryegrass-herbaceous type (Table 3) was dominated by ryegrass

(*Lolium multiflorum* Lam.), watercress (*Rorippa nasturium-aquaticum* [L.] Hayek), and toad rush (*Juncus bufonius* L.). This type averaged 43% total grass cover and 13% total forb cover. Total vegetation cover averaged 71%, ranging between 35% and 100% cover (herbaceous + shrubs + trees). Only 39% of the springs in this type maintained a tree overstory, and only 36% of the plots in this type maintained a shrub component.

Elevation averaged 376 m (128–817 m), textural classes were primarily somewhat poorly drained clay loams. Thirty-three of the 36 sample springs in the Ryegrass-herbaceous type were grazed by cattle.

Rush-herbaceous type.—The Rush-herbaceous type (Table 4) was characterized by the presence of two rush species: common rush (*Juncus patens* E. Meyer) and *J. xiphioides* E. Meyer. Ryegrass was still a common component, and willows occurred on about 5 of the 11 plots in the type. Sedges (*Carex* spp.), American speedwell (*Veronica americana* [Raf.] Benth.), and field horsetail (*Equisetum avense* L.) also occurred frequently. The Rush-her-

TABLE 4. RUSH-HERBACEOUS TYPE DESCRIPTIVE STATISTICS. Constancy equals the number of species occurrences/total number of plots; cover equals the mean cover (%) of a species for a given type (T = trace or <1%); and range equals the range of cover values.

		Con- stancy	Cover	Range
Characteristic plant taxa				
<i>Salix</i> spp.	willow	45	46	1-100
<i>Rhamnus californica</i> Eschsch.	California coffeeberry	27	14	3-24
<i>Rubus ursinus</i> Cham. & Schldl.	California blackberry	55	10	5-15
<i>Lolium multiflorum</i> Lam.	ryegrass	73	3	T-8
<i>Juncus patens</i> E. Meyer	common rush	73	3	T-10
<i>Juncus xiphioides</i> E. Meyer	iris-leaved rush	73	5	T-16
<i>Veronica americana</i> (Raf.) Benth	American speedwell	64	6	2-14
<i>Carex</i> spp.	sedge	64	7	2-16
<i>Equisetum arvense</i> L.	field horsetail	55	17	T-35
<i>Juncus effusus</i> L.	bog rush	45	8	3-14
<i>Mimulus guttatus</i> DC.	common monkeyflower	45	5	1-18
<i>Conium maculatum</i> L.	poison hemlock	36	3	2-6
<i>Juncus bufonius</i> L.	toad rush	36	1	T-3
<i>Rorippa nasturium-aquatica</i> (L.) Hayek	watercress	27	4	2-6
<i>Picris echioides</i> L.	bristly oxtongue	27	1	T-2
<i>Bromus diandrus</i> Roth	ripgut brome	27	4	2-8
<i>Cynara cardunculus</i> L.	artichoke thistle	27	9	5-14
Biotic environment				
Total Vegetative Cover (%)	83 (55-100)			
Tree Cover (%)	57 (1-100) n = 8			
Shrub Cover (%)	22 (1-57) n = 8			
Grass Cover (%)	29 (10-50) n = 10			
Forb Cover (%)	22 (1-65) n = 11			
Abiotic environment				
Elevation (m)	253 (128-402)			
Slope (%)	21 (10-32)			
Aspect	NW primarily			
Position	Upper and mid slopes, draws			
Bare (%)	19 (3-50) n = 10			
Rock (%)	3 (2-4) n = 2			
Soil Series	Los Gatos primarily			
Texture	Loams			
Coarse Fragments (%)	11 (4-15) n = 3			
Rootability	Hard & massive, hard & fractured			
Soil Drainage	Somewhat well to poorly drained			

baceous spring type was distinguished from the Ryegrass-herbaceous type by the presence of sedges and horsetail, as well as the occurrence of California blackberry (*Rubus ursinus* Cham. & Schldl.) and/or a woody overstory. Total vegetation cover averaged 83%, which is similar to the Ryegrass-herbaceous type. Tree and/or shrub cover was found on this type about 73% of the time, and when found, averaged 57% and 22% cover, respectively.

The Rush-herbaceous type was found at an average elevation of 253 m (128-402 m) on loamy textured soils. Three of the 11 plots classified as Rush-herbaceous were ungrazed.

Willow-Poison oak type.—The Willow-Poison oak type (Table 5) was dominated by willows. On plots without willow, blue elderberry (*Sambucus mexicana* C. Presl) was often present. Poison oak (*Toxicodendron diversilobum* [Torrey & A. Gray] E. Greene) was common, occurring on 73% of the

11 sample plots classified in this type. The herbaceous understory was sparse with total graminoid cover averaging 19%, and forb cover averaging 8%. Shrub cover averaged 40% and was found on all plots classified in this type. Tree cover averaged 49% and occurred on all but one plot in this type where the shrub coffeeberry (*Rhamnus californica* Eschsch.) was found.

The Willow-Poison oak type occurred on sites averaging 254 m (116-536 m) elevation. Soils were predominantly loams, and 5 of 11 sites in this type were ungrazed.

California bay-Poison oak type.—The California bay-Poison oak type (Table 6) was dominated by California bay. Coast live oak was present as the overstory species at the one site in this type that did not contain California bay. This type also contained Poison oak, blackberry, mosses, and occasionally chainfern (*Woodwardia fimbriata* Smith).

TABLE 5. WILLOW-POISON OAK TYPE DESCRIPTIVE STATISTICS. Constancy equals the number of species occurrences/total number of plots; cover equals the mean cover (%) of a species for a given type; and range equals the range of cover values (T = trace or <1%).

		Con- stancy	Cover	Range
Characteristic plant taxa				
<i>Salix</i> spp.	willow	73	42	25–56
<i>Sambucus mexicana</i> C. Presl	blue elderberry	27	9	4–18
<i>Toxicodendron diversilobum</i> (Torrey & A. Gray) E. Greene	poison oak	73	26	1–64
<i>Baccharis pilularis</i> DC.	baccharis	45	20	T–59
<i>Rubus ursinus</i> Cham. & Schldl.	California blackberry	45	23	2–60
<i>Lolium multiflorum</i> Lam.	ryegrass	36	2	T–4
<i>Bromus diandrus</i> Roth	ripgut brome	27	7	3–13
<i>Carex</i> spp.	sedge	27	2	T–3
Biotic environment				
Total Vegetative Cover (%)	85 (50–95)			
Tree Cover (%)	49 (5–93) n = 10			
Shrub Cover (%)	40 (5–80) n = 11			
Grass Cover (%)	19 (1–50) n = 11			
Forb Cover (%)	8 (1–35) n = 11			
Abiotic environment				
Elevation (m)	286 (116–536)			
Slope (%)	21 (5–58)			
Aspect	SE, SW			
Position	Upper, mid, lower slopes			
Bare (%)	33 (5–60) n = 10			
Rock (%)	14 (1–20) n = 3			
Soil Series	Los Osos, various			
Texture	Loams			
Coarse Fragments (%)	19 (1–60) n = 4			
Rootability	Primarily hard & massive			
Soil Drainage	Primarily well drained			

Total vegetation cover averaged 91%. Graminoid and forb cover was very low, 5% and 11% respectively. Tree cover averaged 83% and was found on all plots in this type. Seventy-five percent of the plots in this type maintained shrub cover which averaged 32% when present.

Elevation ranges for this type were 122 to 658 m with an average of 394 m. Grazing occurred at two of the 12 sites in this type. The textural class of these soils was primarily loams.

Environmental and management factors. CCA ordination axes showed that at least 3 significant orthogonal gradients could be created by taking the linear combination of environmental variables (Table 7). Axis 1 (CCA₁) was most closely correlated with the variable LITTER. The California bay-Poison oak type scored high on this vector compared to the other 3 vegetation groups (Fig. 3a).

CCA₂ was correlated with ELEVATION primarily; however, the two categorical variables LOAM and CLAYLOAM were also useful in creating this axis (Table 7). Though CCA₂ helped disperse the species matrix as a whole, indicating a strong underlying gradient, it provided minimal insight into the separation of vegetation types. Willow-Poison oak sites generally scored positively while the

Rush-herbaceous type appeared at mainly below-average elevations.

Finally, CCA₃ separated sites within all four vegetation types (Figs. 3b, c) apparently for the presence or absence of grazing (Table 7). However, only 2 California bay-Poison oak sites scored positively (indicating no grazing) on CCA₃ (Fig. 3c), contrasting CCA₂ and CCA₃.

Three DCA axes were also extracted from the species matrix whose very high eigenvalues indicated 3 underlying gradients that were not completely explained by linear combinations of our environmental and management variables, i.e., DCA found even stronger gradients than CCA (Table 7). This indicated an under-specified explanatory model for this species matrix. Classical indirect gradient analysis would continue from this point by inferring causes of these gradients. Figure 4a shows that DCA₁ arrays our TWINSpan-derived vegetation groupings from overstory to herbaceous types with little overlap, while DCA₂ separates the higher-elevation California bay-Poison oak sites from the middle-elevation Willow-Poison oak and Ryegrass-herbaceous types. Rush-herbaceous sites tended to be located at lower elevations, which is also reflected in Figure 4a. There is no evidence from Figures

TABLE 6. CALIFORNIA BAY-POISON OAK TYPE DESCRIPTIVE STATISTICS. Constancy equals the number of species occurrences/total number of plots; cover equals the mean cover (%) of a species for a given type; and range equals the range of cover values (T = trace or <1%).

		Con- stancy	Cover	Range
Characteristic plant taxa				
<i>Umbellularia californica</i> (Hook. & Arn.) Nutt.	California bay	92	57	16–100
<i>Quercus agrifolia</i> Nee	coast live oak	50	44	10–95
<i>Acer macrophyllum</i> Pursh	big leaf maple	25	17	1–32
<i>Toxicodendron diversilobum</i> (Torrey & A. Gray) E. Greene	poison oak	75	23	T–20
<i>Rubus ursinus</i> Cham. & Schldl.	California blackberry	42	6	3–17
moss	moss	42	4	1–17
<i>Galium aparine</i> L.	common bedstraw	25	1	T–3
<i>Woodwardia fimbriata</i> Smith	chainfern	25	11	4–25
Biotic environment				
Total Vegetative Cover (%)	91 (75–100)			
Tree Cover (%)	83 (45–100) n = 12			
Shrub Cover (%)	32 (1–60) n = 9			
Grass Cover (%)	5 (1–15) n = 10			
Forb Cover (%)	14 (1–40) n = 11			
Abiotic environment				
Elevation (m)	394 (122–658)			
Slope (%)	30 (10–65)			
Aspect	All			
Position	Upper, mid, lower slopes			
Bare (%)	27 (7–65) n = 12			
Rock (%)	3 (2–7) n = 6			
Soil Series	Los Osos, various			
Texture	Loams			
Coarse Fragments (%)	34 (20–60) n = 4			
Rootability	Primarily fractured			
Soil Drainage	Excessively well to poorly drained			

4b and 3c that DCA₃ is a grazing gradient as determined for CCA₃ based on its high correlation with GRAZED. Caution must be used when interpreting correlations between ordination axes and binary variates. Hence we examined a scatterplot of grazed and ungrazed sites distributed along DCA₃

that showed the fewer number of ungrazed sites to be randomly distributed with a narrow range among the many grazed sites that exhibited a much wider range of distribution along DCA₃ (Fig. 5).

Figure 6 shows selected taxa arrayed along CCA₂ and CCA₃. The dotted line indicates where in species space ungrazed sites were found vis-à-vis grazed sites; there was no overlap. Overstory willows (oSALIX), blackberry shrub (sRUUR), and herbaceous layer Poison oak (hTODI) scored highly on CCA₃ concomitant with ungrazed plots. While willows were also found on the grazed plots, they tended to be found as sSALIX—willows in a shrub state. Other overstory taxa were found on grazed plots as California bay (oUMCA) and Coast live oak (oQUAG). Herbaceous taxa were distributed along the negative side of the CCA₃ axis with Italian ryegrass (hLOMU) and common monkeyflower (hMIGU) scoring highest for grazed plots and sedges (hCAREX) and rushes (hJUXI, hJUEF) scoring moderately.

DISCUSSION

DCA axes displayed three much stronger underlying gradients than CCA axes exposed, making it

TABLE 7. ORDINATION RESULTS. ¹ 180–azimuth.

	Axis 1	Axis 2	Axis 3
CCA Results			
Eigenvalue (λ)	0.487	0.415	0.363
P	0.02	0.01	0.01
Intraset correlations			
ELEVATION	−0.312	−0.554	−0.436
ASPECT ¹	−0.156	0.486	−0.221
SLOPE	−0.342	−0.207	−0.018
LOAM	−0.416	−0.445	0.341
CLAYLOAM	0.321	0.428	−0.579
LITTER	−0.834	0.062	0.156
BARE	−0.211	0.276	−0.153
GRAZING	0.192	−0.006	−0.852
DCA Results			
Eigenvalue (λ)	0.765	0.636	0.547

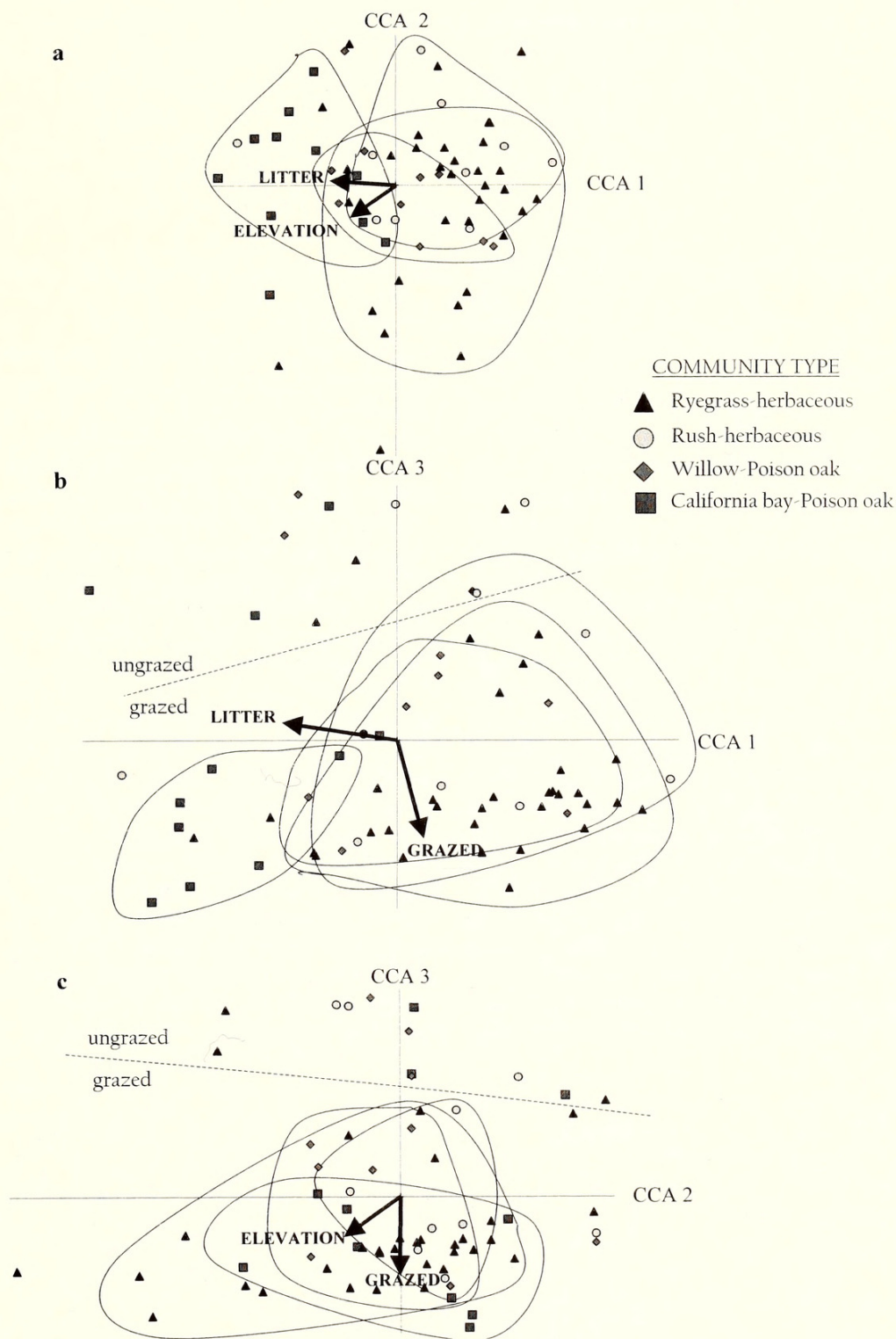


FIG. 3. Canonical correspondence analysis (CCA) joint-plots contrasting each of 3 orthogonal ordination axes. All sites above dotted line were ungrazed; all sites below were grazed. Note: polygons not inclusive of all sites from a given community type.

clear that the CCA model was under-specified, i.e., one or more driving factors were not included. CCA₁'s correlation with litter quantity indicated a productivity gradient from the relatively low-productivity annual grass-dominated Ryegrass-herbaceous type to the high biomass tree types—California bay-Poison oak and Willow-Poison oak. This spread seems indicative of a gradient driven by water availability. Ryegrass is an annual species that

fares well on dry uplands as well as on areas that undergo periodic inundation throughout California, while rushes tend to be hydrophilic taxa existing in topographic depressions, seeps, and springs (Bowerman 1944; Keator 1994). At lower elevation spring sites, water availability is likely to be more constant than at higher elevation sites due to greater upslope catchment area. Hence, these lower elevation sites with even greater water availability and

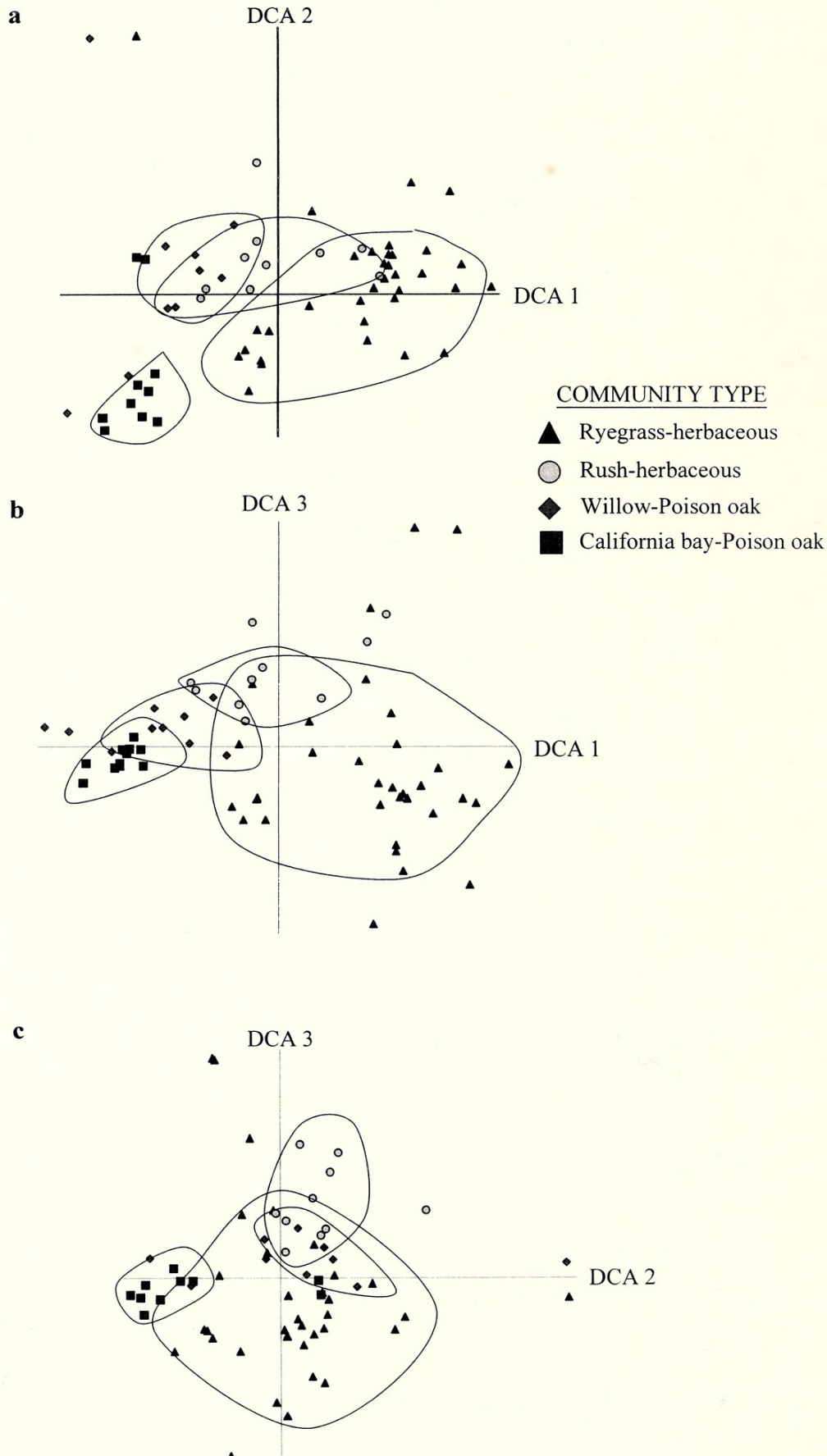


FIG. 4. Detrended correspondence analysis (DCA) joint-plots contrasting each of 3 orthogonal ordination axes. Note: polygons not inclusive of all sites from a given community type.

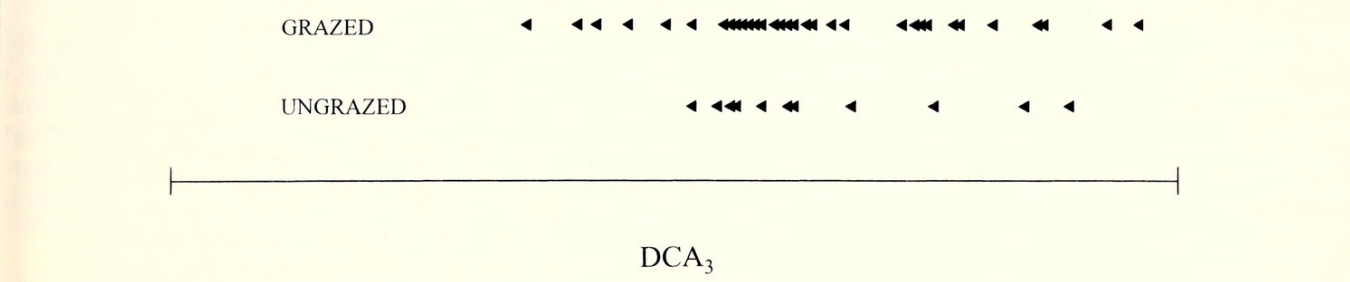


FIG. 5. Distribution of ungrazed and grazed sites along the third detrended correspondence analysis gradient (DCA₃).

probably higher flows support willows. Willows are known to use stream water in addition to soil water to compete effectively with herbaceous vegetation, which uses soil water only (Alstad et al. 1999). Finally, it was not surprising that the California bay-Poison oak type scored high for greater litter levels since California bay is known for recalcitrant, slowly decomposing leaves-due to its relatively high concentrations of phenolic secondary compounds, (Goralka and Langenheim 1995). California bay-Poison oak sites also often maintained a coffeeberry or blackberry shrub component adding to the high productivity.

CCA₂ indicated a strong gradient, orthogonal to the productivity gradient discussed above (CCA₁), that appeared tied to elevational differences among sites. However, the categorical soil texture variables LOAM and CLAYLOAM each showed high correlations with CCA₂ as well. Visual examination of Figures 3a and 3c showed that while CCA₂ strongly separated some of the individual species, it did not disperse our four plant groupings very well. Perhaps some species wax and wane with temperature fluctuations that vary with elevation while the dominant taxa (which defined the vegetation types) re-

main. Also, the coarseness of our soil texture variables may play a role in the relative ambiguity of the gradient represented by CCA₂.

The correlation coefficients for LOAM and CLAYLOAM showed opposite signs with respect to CCA₂. LOAM corresponded roughly to higher elevations and CLAYLOAM to lower sites indicative of greater soil weathering via periodic inundation.

CCA₃ appeared to represent a species ordination related to the presence or absence of livestock grazing. Interestingly, three plots from each type were ungrazed and all scored highly on CCA₃ indicating that these sites all had something in common vegetatively. A popular notion is that livestock grazing degrades riparian areas and especially remove the willow component. The presence of willow at both grazed and ungrazed sites argues against this notion at first glance. Of the ten sites classified as Willow-Poison oak, six were grazed. What seems clear from Figure 6 is that while willows were present at both grazed and ungrazed sites, their size-classes were likely affected so that grazed sites maintained more of a willow shrub component, while ungrazed sites were more likely to maintain willows in the

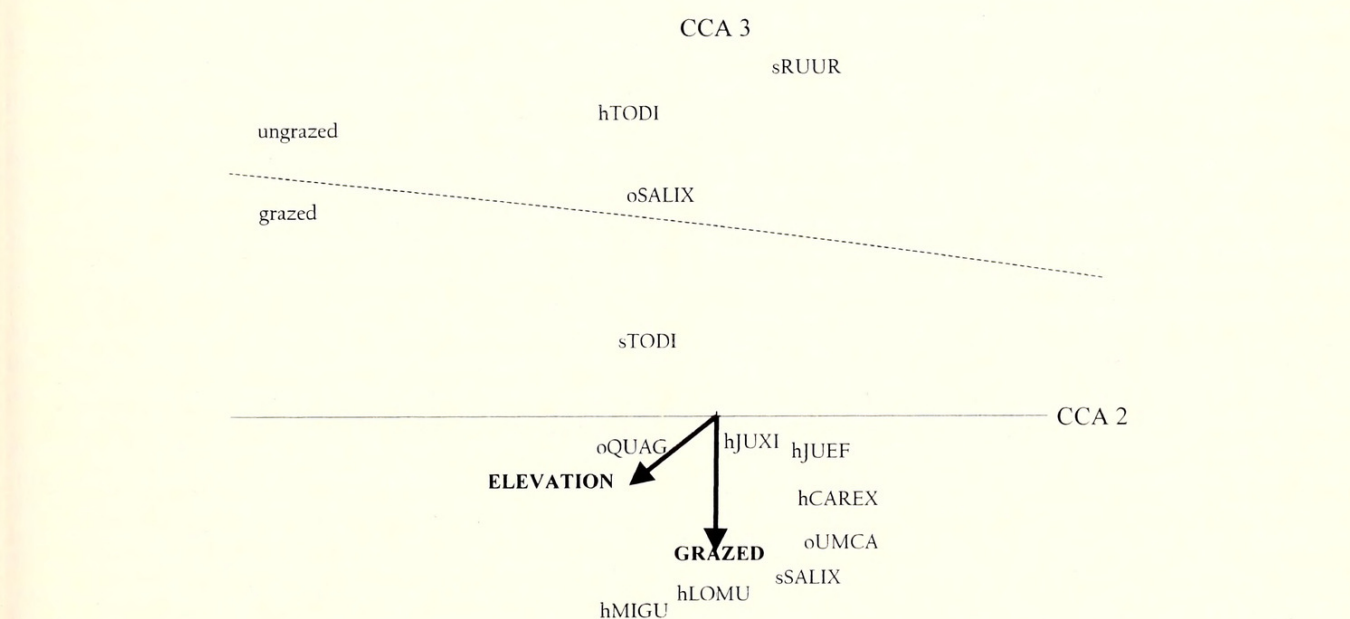


FIG. 6. Canonical correspondence analysis (CCA) joint-plot (same as Figure 3c) showing selected taxa with associated vertical layer prefix, i.e., herbaceous (h), shrub (s), or overstory (o). Taxa are: RUUR—*Rubus ursinus*, TODI—*Toxicodendron diversiloba*, SALIX—*Salix* spp., QUAG—*Quercus agrifolia*, JUXI—*Juncus xiphioides*, JUEF—*J. effusus*, CAREX—*Carex* spp., UMCA—*Umbellularia californica*, MIGU—*Mimulus guttatus*, LOMU—*Lolium multiflorum*.

overstory. These results align with Peinetti et al. (2001) who showed willow productivity was unaffected by large herbivores, but that overall morphology shifted to more prostrate growth forms with grazing. They further concluded that the temporal distribution of grazing was important in determining these effects.

Another conspicuous pattern emerging from the 4 ungrazed Willow-Poison oak sites was the high cover of blackberry in the shrub layer (often >40% cover) and the herbaceous layer (~5–20% cover). We have also observed the conversion of herbaceous spring sites to blackberry shrub dominance that completely eliminates the herbaceous component at Sierra Nevada oak woodland springs (B. Allen-Diaz unpublished data).

Interestingly, both the Ryegrass-herbaceous and the California bay-Poison oak types scored positively for grazing (negatively on CCA₃) showing that both life-form types (herbaceous and overstory) were extant under this management scenario. More detailed information about grazing management (intensity and temporal distribution) under experimental designs needs to be applied before conclusions about grazing effects on spring types can be verified. Livestock grazing has been implicated in general riparian area degradation (Fleischner 1994; Belsky et al. 1999), but has also received credit for ameliorating streambank slumping (Myers and Swanson 1992) and freshwater fish habitat (Knapp et al. 1998). Allen-Diaz and Jackson (2000) showed that light to moderate grazing intensity (based on upland residual dry matter estimates) resulted no compositional shifts on Sierra Nevada oak woodland springs. Certainly, overgrazing (unsustainable grazing pressure), will induce a cascade of deleterious effects on ecosystems, i.e., bank erosion, vegetation loss, reduced stream water quality (Belsky et al. 1999), however, there is neither casual nor scientific indication that either of the two land management agencies discussed here practice overgrazing.

Grazing presence/absence does not appear to influence the community type overall (i.e., composition) but may have important within-type effects on the vegetative structure when willows are present. Other overstory taxa did not show this pattern.

By using quantitative, quasi-objective classification analysis, we were able to delimit four spring-fed plant community types for the East Bay Hills, California. Finer scale description would certainly provide a greater number of community types; these four appeared to repeat strongly across these landscapes. These results should not be taken as evidence that livestock grazing has no important effects on these systems—only well designed field experiments will inform these questions. However, these results should provide useful information to those designing and implementing future experiments and surveys. Other California landscapes and regions containing similar and disparate spring

types also need delineation. For instance, we did not observe the ubiquitous cattail type (*Typha* spp.) so often observed in Sierra Nevada foothill oak woodlands. Community types should be described on a site-specific basis in order to more fully characterize variability within and among these patch ecosystems.

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