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CANOPY GAPS, ZONATION AND TOPOGRAPHY STRUCTURE: A NORTHERN COASTAL SCRUB COMMUNITY ON CALIFORNIA COASTAL BLUFFS

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ABSTRACT

We examined northern coastal scrub vegetation in relation to canopy gap formation, zonation and topographic relief on coastal escarpments (bluffs) in San Mateo County, CA. Vegetation was sampled in quadrats, along line transects and within gaps in the canopy of the dominant shrub *Baccharis pilularis* DC. (*Baccharis* gaps) on three topographically distinct coastal bluffs. *Baccharis* gaps were also sampled for area, light penetration, distance from the bluff edge, and residual branch height. Thirty-seven species were encountered in quadrats at the three sampling sites. *Baccharis pilularis* and *Eriophyllum staechadifolium* Lagasca were the dominant species, together comprising 67% cover at the three sites. Canopy gaps averaged 0.96 m^2 in area and occupied 58% of the area sampled. Species composition and relative abundance was strongly influenced by percent canopy gap. Cover of *Scrophularia californica* Cham. & Schldl. was found to increase with increasing percent canopy gap. Thirty-eight percent of species occurred exclusively in quadrats dominated by canopy gaps. Species richness showed a positive relationship to percent canopy gap and to *Baccharis* gaps with greater light penetration. Line transects indicated distinct species and gap zonation on the three bluff sites sampled. Differences in species composition, species relative abundance and vegetation height were also found among the three coastal bluff sites. At the spatial scale of an individual bluff, our results suggest that canopy gaps and zonation are important in maintaining the diversity of northern coastal scrub in San Mateo County. Variation in topographic relief among neighboring bluff sites also appears to play a role in maintaining species diversity at larger spatial scales.

Northern coastal scrub occurs in a narrow and discontinuous region along the Pacific coast of North America from southern Oregon to Point Sur, Monterey Co., CA (Munz and Keck 1968; Ornduff 1974; Heady et al. 1988). The vegetation is characterized by low (<2 m) shrubs and a conspicuous herbaceous component (Heady et al. 1988). Throughout much of its range, northern coastal scrub occurs with coastal prairie and together they form a mosaic that is interrupted by oak woodland, mixed evergreen forest, closed-cone pine forest and fresh and saltwater marshes (Ornduff 1974; Axelrod 1978; Bakker 1984; personal observation).

Few studies have examined the community structure and diversity of northern coastal scrub vegetation. These investigations have focused on scrub invasion of grassland (McBride and Heady 1968; Hobbs and Mooney 1986; Williams et al. 1987), the effects of fire and grazing suppression (Elliot and Wehausen 1974; McBride 1974) and vegetation patterns in relation to slope-aspect (Grams et al. 1977), salt spray (Barbour 1978; Holton Jr. and Johnson 1979), and north-south range transitions (Heady et al. 1988).

There is little information on northern coastal scrub community structure and diversity in distinctly maritime locations in central California (but see Barbour 1978; Holton Jr. and Johnson 1979). Here, northern coastal scrub occurs on a topographically diverse system of coastal escarpments, or bluffs. These bluffs are exposed to different intensities of wind, solar radiation and sea-salt deposition, each of which can influence plant community structure (Boyce 1954; Malloch 1972; Barbour 1978; Holton Jr. and Johnson 1979). Northern coastal scrub on coastal bluffs is distinct in species composition and physiognomy from that occurring inland (Heady et al. 1988). The vegetation in many locations is prostrate (≤0.2 m) and large openings (gaps) in the canopy of the dominant shrub, *Baccharis pilularis* DC., are a prominent feature of the scrub vegetation. These patterns, and the factors responsible for creating them, have not been well studied, nor has their influence on plant diversity been investigated.

We investigated the influence of canopy gaps, zonation, and topographic relief on northern coastal scrub community structure and diversity on coastal escarpments in San Mateo Co., CA. We hypothesized that canopy gaps play a role in maintaining species diversity at a local spatial scale (i.e., within individual bluffs). To test this hypothesis, we investigated the relationship between the extent of canopy gaps and species composition, relative abundance and richness. In addition, we examined the relationship between gap structure and species diversity. We also hypothesized that coastal scrub

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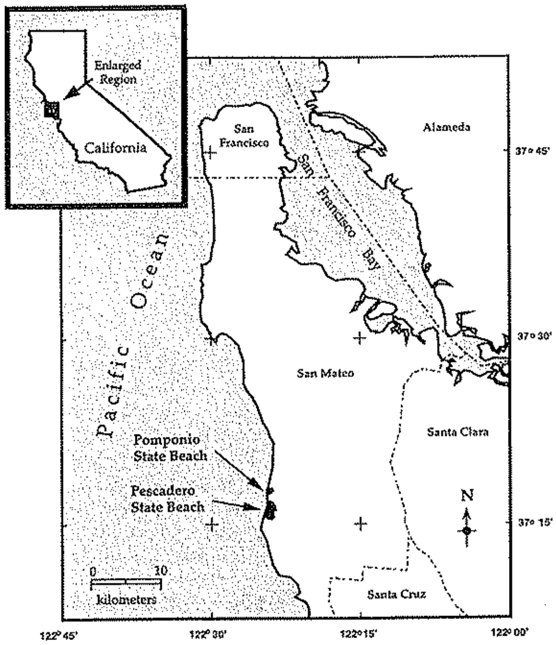

FIG. 1. Location of the three bluff sites studied. Site 2 was located at Pomponio State Beach and Sites 1 and 3 were located at Pescadero State Beach.

species would show zonation with respect to distance from the bluff edge. This hypothesis was tested by sampling vegetation along line transects extending away from the cliff edge. Finally, we hypothesized that variation in topographic relief among coastal bluffs is important in maintaining species diversity at larger spatial scales. This hypothesis is based on the assumption that differences in topographic relief among bluffs should expose individual escarpments to distinct environmental conditions (e.g., wind impact, solar radiation, and salt spray deposition), thereby altering scrub community composition. To examine this we compared bluff sites with respect to species composition and abundance.

STUDY AREA

Physical environment. This study was conducted within Pescadero and Pomponio State Beaches in San Mateo Co., CA. (37°17′N, 122°24′W) (Fig. 1). The study sites were located on coastal terrace escarpments derived from uplifted Pleistocene marine sediments of mixed origin (Wagner and Nelson 1961). Coastal terrace escarpments, or bluffs, are a common topographic feature along this coast and range widely in elevation, slope and aspect. Bluffs in this region may range in elevation from 20 to 50 m, with cliffs at their coastal margins.

The climate is Mediterranean, with mild, wet winters and warm, dry summers. Due to the maritime influence, temperatures are cool year round. At San Gregorio, approximately 5 km north of the study sites, mean annual temperature is 13°C (U.S. Weather Bureau 1979–1989). Temperatures range from a monthly mean low of 10°C in January, to a monthly mean high of 16°C in August. Mean annual precipitation at San Gregorio is 773 mm, with over 95% falling between September and April (U.S. Weather Bureau, 1979–1989). Although official records are not kept on its occurrence, summer fog is common along the central California coast and may provide additional moisture in the form of fog drip.

North-northwesterly winds are constant, with the highest velocities in winter and spring. Average wind speed is 21.7 km/h at Pescadero (California Surface Wind Climatology 1992). Sea-salt aerosols are carried by the wind and deposited on the soil and vegetation (Clayton 1972; Barbour 1978).

Vegetation. Northern coastal scrub is composed of a diverse community of shrubs, perennial herbs, and vines. Characteristic species include *Baccharis pilularis, Eriophyllum staechadifolium* Lagasca, *Gaultheria shallon* Pursh, *Eriogonum latifolium* Smith, *Erigeron glaucus* Ker-Gawler, *Heracleum lanatum* Michaux, *Anaphalis margaritacea* (L.) Benth. & Hook., and *Rubus* spp. On the San Mateo Co. coast, the physiognomy and species composition of northern coastal scrub differ as a function of exposure to ocean influence (Clayton 1972). The vegetation on the immediate coast is lower in stature (<1 m) than shrubland several hundred meters from the beach (Clayton 1972; Heady et al. 1988; personal observation). A prostrate form of *Baccharis pilularis,* which was noted by Hoover (1970) in San Luis Obispo Co., by Clayton (1972) in San Mateo Co., and by Holton Jr. and Johnson (1979) at Point Reyes Peninsula, also occurs on these bluffs and ranges from extremely prostrate (<0.1 m) to approximately 1 m in height.

Openings in the vegetation canopy are a prominent feature of northern coastal scrub on coastal bluffs in San Mateo Co. (Fig. 2). We refer to these openings as canopy gaps and define them as contiguous regions within one or more shrubs of the same species that are virtually devoid of leaves and ≥ 0.2 m in diameter. Although the individual shrub in which a canopy gap occurs may be alive or dead, branches are generally still present within gaps. Canopy gaps occur primarily within the crowns of live *B. pilularis.* Although less frequent, gaps also occur in *E. staechadifolium* and *Lupinus arboreus* Sims.

METHODS

Site selection. Three bluff sites were chosen that differed in slope, aspect and apparent exposure to wind and sea-salt deposition (Table 1, Fig. 1). The three sites were numbered in order of presumed maritime influence, Site 1 being the most exposed and Site 3 the least. Sites were intact stands of

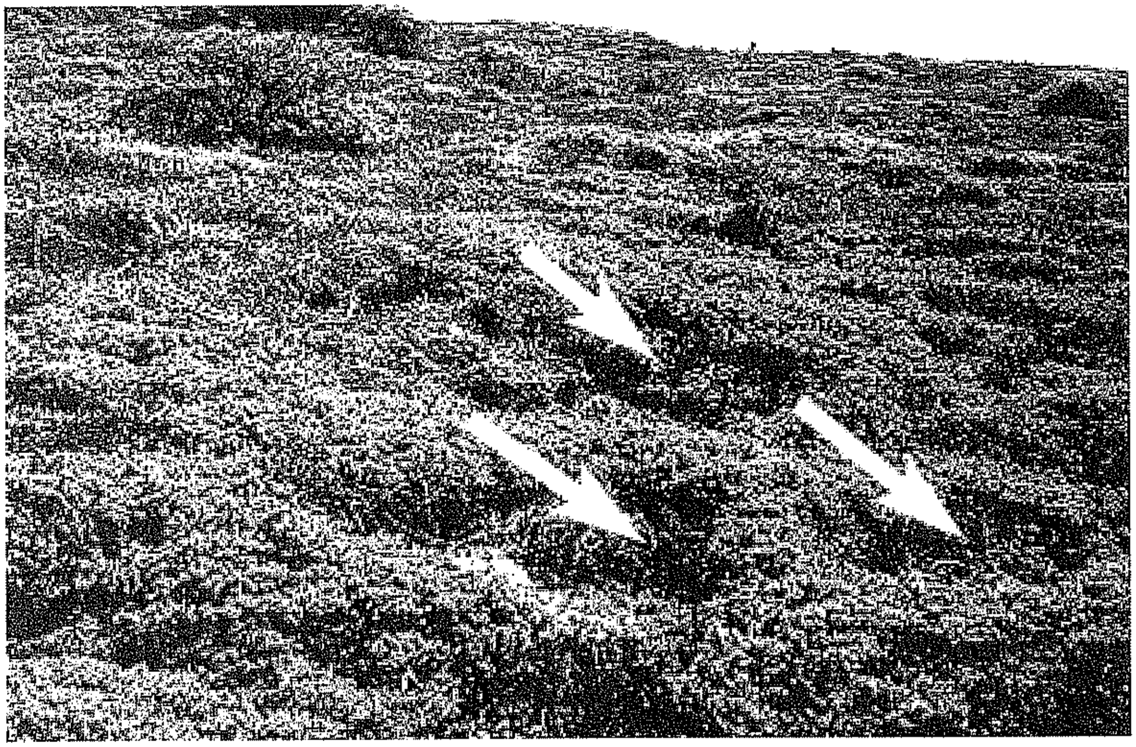

FIG. 2. Site 2, showing the extent and distribution of *Baccharis* gaps. Arrow indicates a *Baccharis* gap.

northern coastal scrub that showed minimal signs of human disturbance.

Vegetation sampling. To examine the role of canopy gaps, zonation, and topography on plant species distribution and diversity, we sampled vegetation in quadrats, along line transects and within individual gaps in the canopy of *Baccharis pilularis*. We refer to these gaps as *Baccharis* gaps. Sampling was completed between April and July 1992.

Quadrats. We estimated species relative percent cover and percent frequency from fifty-eight 1 × 0.75 m quadrats. Vegetation height and distance from the cliff edge were also determined for each quadrat. In addition, the proportion of a quadrat constituting a canopy gap (i.e., percent gap), as previously defined, was estimated. Canopy gaps were classified as "*Baccharis* gaps," if they occurred within this shrub, or "Other gap." Sites were sampled in a stratified random fashion to ensure adequate representation of each site. Eight quadrats were sampled at Site 1, thirty-two quadrats at Site 2, and eighteen at Site 3. Species area curves for each site indicated that samples adequately captured the diversity present.

Throughout this study, the presence of unstable cliffs at Site 1 and the position of Site 3 on the bluff required that we sample these sites at 7 and 24 m from the cliff edge, respectively. A more stable bluff at Site 2 allowed sampling up to 0.5 m from the cliff edge.

Line transects. We examined zonation by sampling vegetation and canopy gaps along line transects at each site. Three transects per site were randomly placed, running parallel to the direction of

TABLE 1. AREA, ELEVATION, SLOPE AND ASPECT OF THE THREE COASTAL BLUFF SITES STUDIED. * NA = not applicable.

Site	Area (ha)	Elevation (m)	Slope	Aspect
1	0.1	37	20°	275°
2	0.5	45	0°	NA*
3	0.2	38	8°	90°

TABLE 2. DEFINITIONS OF THE 3 CLASSES USED TO INDEX RELATIVE LIGHT PENETRATION IN *BACCHARIS* GAP SAMPLES.

Gap class	Definition
1	None to very few branches within the gap; maximum light penetration at the soil level.
2	Moderate density of small diameter branches within the gap; moderate light penetration at the soil level.
3	High density of small branches within the gap; low light penetration at the soil level.

TABLE 3. SPECIES RELATIVE COVER (% COVER) AND FREQUENCY (% FREQ.) AT EACH SITE AND FOR ALL SITES COMBINED. Cover and frequency values were determined from quadrat samples. No entry indicates that the species was not encountered.

Species	Site 1		Site 2		Site 3		All sites	
	% Cover	% Freq.	% Cover	% Freq.	% Cover	% Freq.	% Cover	% Freq.
Shrubs								
Baccharis pilularis	24.3	100	59.8	94	32.3	89	46.4	93
Eriophyllum staechadifolium	19.7	100	5.9	44	49.2	89	20.2	66
Lupinus arboreus	—	—	0.5	16	—	—	0.3	9
Artemisia californica	—	—	0.8	3	—	—	0.5	2
Perennial Herbs								
Erigeron glaucus	7.9	50	14.3	72	—	—	9.3	47
Achillea millefolium	1.7	38	3.4	53	4.8	50	3.5	50
Scrophularia californica subsp. *californica*	2.2	63	5.3	34	1.7	11	3.8	31
Iris douglasiana	9.2	75	0.2	3	—	—	1.6	12
Castilleja latifolia	—	—	1.1	16	—	—	0.6	9
Aster lentus	0.6	13	0.6	6	0.7	6	0.6	7
Angelica hendersonii	3.7	25	—	—	—	—	0.6	3
Solidago canadensis subsp. *elongata*	4.5	13	—	—	—	—	0.7	2
Horkelia californica subsp. *californica*	—	—	—	—	0.9	6	0.3	2
Stachys ajugoides subsp. *rigida*	0.5	13	—	—	—	—	<0.1	2
Gnaphalium purpureum	—	—	<0.1	3	—	—	<0.1	2
Gnaphalium stramineum	—	—	<0.1	3	—	—	<0.1	2
Perennial Vines								
Rubus ursinus	6.8	38	1.0	6	—	—	1.7	9
Satureja douglasii	4.0	13	1.2	9	—	—	1.3	7
Carpobrotus edulis	—	—	0.4	3	—	—	0.2	2
Perennial Grasses								
Agrostis densiflora	—	—	<0.1	3	0.2	6	0.1	3
Bromus carinatus var. *maritimus*	—	—	0.5	6	—	—	0.3	3
Deschampsia elongata	—	—	<0.1	3	—	—	<0.1	3
Perennial Rushes/Sedges								
Juncus patens	1.4	38	2.1	19	—	—	1.4	16
Juncus sp.	—	—	—	—	0.5	6	0.1	2
Carex obnupta	—	—	1.3	9	—	—	0.7	5
Carex sp.	—	—	<0.1	3	—	—	<0.1	2
Ferns								
Polypodium californicum	4.8	38	—	—	—	—	0.8	5
Dryopteris arguta	0.3	13	—	—	—	—	<0.1	2

TABLE 3. CONTINUED

Species	Site 1 % Cover	Site 1 % Freq.	Site 2 % Cover	Site 2 % Freq.	Site 3 % Cover	Site 3 % Freq.	All sites % Cover	All sites % Freq.
Annual Herbs								
Daucus pusillus	0.2	13	<0.1	3	—	—	<0.1	3
Centaurium davyi	—	—	<0.1	3	—	—	<0.1	2
Sonchus asper subsp. *asper*	—	—	<0.1	3	—	—	<0.1	2
Annual Vines								
Galium aparine	3.8	63	—	—	4.5	67	1.9	29
Pterostegia drymarioides	2.7	75	—	—	1.6	28	0.9	19
Anagallis arvensis	0.8	25	0.1	6	1.7	33	0.7	17
Annual Grasses								
Vulpia bromoides	0.8	25	0.9	28	1.9	17	1.1	24
Agrostis sp.	—	—	<0.1	6	<0.1	6	<0.1	3
Aira caryophyllea	—	—	<0.1	6	—	—	<0.1	2

the prevailing north-northwesterly winds (~135°). Transects were 20 m at Site 1 and 30 m at Sites 2 and 3. Percent vegetation cover, percent gap, and vegetation height were recorded in 0.5 m units along transects.

Baccharis *gaps.* We sampled canopy gaps occurring in *B. pilularis* to investigate relationships between gap structure and species diversity. Fifty-eight *Baccharis* gaps were sampled at the three bluff sites, eight at Site 1, thirty-two at Site 2, and eighteen at Site 3. *Baccharis* gaps were selected within sites in a stratified random fashion. Gap area (m^2), height of the branch material within gaps, and distance to the nearest cliff edge were recorded for each gap. In addition, *Baccharis* gaps were assigned to one of 3 classes, which indexed the relative degree of light penetration into the gap. *Baccharis* gap classes are defined in Table 2.

Data analyses. We used principal component analysis (PCA) and multivariate analysis of covariance (MANCOVA) to test differences in community composition and relative abundance among sites and with respect to percent canopy gap. In the PCA we used a variance-covariance matrix with cover values of species that occurred more than once in the data set (i.e., 24 species, accounting for 98% of total plant cover). The broken-stick method was used to determine the number of axes retained (Jackson 1993). We then used the principal component scores of the first two principal component axes in a MANCOVA to test community-level differences among the three sites and with respect to percent canopy gap (Morin et al. 1990). Percent gap was used as the covariate. Pearson's product moment correlation was used to examine species relationships with the principal component axes.

To evaluate the relationship between species cover and percent canopy gap in quadrat samples, we used regression analysis on arcsine-square root transformed cover values. Regression was also used to assess the relationship between species richness and canopy gap variables as well as between bluff position and vegetation height. We compared species cover and percent canopy gap along line transects using either the Mann-Whitney U test (Site 1) or the Kruskal-Wallis test (Sites 2 and 3). Differences in species richness among the three gap classes were compared using the Kruskal-Wallis test. Tukey's Studentized Range test was used to distinguish treatment means in all parametric analyses. Means in all Kruskal-Wallis tests were distinguished using Dunn's multiple comparison test.

We conducted the PCA using PC-ORD version 3.01 (McCune and Mefford 1997). Parametric analyses were performed using Statistical Analysis Software version 6.12 (SAS Institute 1990). Nonparametric analyses were conducted using GraphPad Prism version 3.00, GraphPad Software, San Diego, CA.

TABLE 4. MEAN (±1 SE) % AREA OCCUPIED AND SIZE OF *BACCHARIS* GAPS AND OTHER GAPS IN VEGETATION SAMPLES AT EACH BLUFF SITE AND FOR ALL SITES COMBINED.

		Sites			
Gap type	Variable	1	2	3	All sites
Baccharis	% Area	53 (10)	49 (5.4)	34 (8.1)	45 (3.7)
	Size (m^2)	0.95 (0.26)	0.97 (0.24)	0.94 (0.16)	0.96 (0.15)
Other	% Area	12 (6.3)	9.4 (5.0)	21 (9.0)	13 (3.5)

RESULTS

General vegetation patterns. Of the thirty-seven plant species encountered in quadrats from the three coastal bluff sites, twenty occurred at Site 1, twenty-seven at Site 2, and thirteen at Site 3 (Table 3). *Baccharis pilularis* and *Eriophyllum staechadifolium* were the dominant species, together comprising 67% cover at the three sites. Other common species encountered in quadrats were the perennial herbs *Erigeron glaucus, Achillea millefolium* L. and *Scrophularia californica* Cham. & Schldl.

Canopy gaps in *B. pilularis* (*Baccharis* gaps) were a common structural feature on the three bluff sites, with 45% of the area sampled occupied by these gaps; Other gaps occupied 13% of the area sampled (Table 4). Although percent area occupied by *Baccharis* gaps and Other gaps varied across sites, no significant differences were detected. *Baccharis* gaps averaged 0.96 ± 0.15 m^2 in area and ranged from 0.14 to 7.68 m^2, with 90% of gaps less than 2 m^2.

Quadrat samples. Overall differences in the scrub community among the three bluff sites are illustrated in a PCA diagram (Fig. 3). The two axes retained in the analysis accounted for 81% of the total variance, with Axis 1 accounting for 60.6% and Axis 2 20.6% of the variance (Table 5). Coastal scrub species composition and abundance differed significantly across the three bluff sites (MANCOVA: $P < 0.001$). Means comparisons showed that Axis 1 distinguished Site 2 from Sites 1 and 3, and Axis 2 distinguished Site 3 from Sites 1 and 2. Based on correlations of individual species in the ordination (Table 5), Axis 1 separated quadrats among sites based on the abundance of *B. pilularis* at Site 2 and *E. staechadifolium* and *Anagallis arvensis* L. at Sites 1 and 3. Likewise, Axis 2 distinguished samples based on the abundance of *E. staechadifolium* at Site 3 versus *E. glaucus* and *S. californica* at Sites 1 and 2.

A highly significant effect of percent canopy gap on plant species composition and abundance was also detected in the MANCOVA ($P < 0.001$). Thus, irrespective of site differences, a substantial amount of variation in species composition and abundance was explained by the extent of canopy gaps. This is illustrated in the PCA diagram (Fig. 3), which distinguishes samples with ≥ 50% canopy gap from those with < 50% canopy gap.

Cover of *S. californica* showed a significant positive relationship to percent canopy gap, as indicated by regression analysis ($R^2 = 0.067$; $P = 0.049$). No significant relationships were observed for other species. However, when quadrats were separated into those with ≥ 50% canopy gap versus those with < 50% canopy gap, fourteen species occurred exclusively in quadrats dominated by canopy gap and were not encountered in other samples. Several of these species are typical coastal prairie species (e.g., *Agrostis densiflora* Vasey, *Centaurium davyi* (Jepson) Abrams, *Agrostis* sp. and *Aira caryophyllea* L.). *Carpobrotus edulis* (L.) N.E. Br., which is an invasive perennial vine in coastal California, was also found only in gap-dominated samples. By contrast three species occurred exclusively in vegetation-dominated quadrats.

Although there was substantial variation in the data, a significant positive relationship was observed between species richness and percent canopy gap in quadrat samples (Fig. 4). Using the 50% cut-off between vegetation- and gap-dominated samples, quadrats with ≥ 50% *Baccharis* gap had a mean of 4.3 ± 0.5 species compared to 2.7 ± 0.3 in the remaining samples (mean ± SE).

TABLE 5. EIGENVECTORS (EIGEN.) AND PEARSON CORRELATION COEFFICIENTS (R) FOR THE FIRST TWO PRINCIPAL COMPONENT AXES DERIVED FROM THE PCA. Species shown were significantly correlated to at least one axis. Eigenvalues for Axis 1 and 2 are 4.28 and 1.44, respectively. Boldface correlation coefficients are significant at $P < 0.05$.

	Axis 1		Axis 2	
Species	Eigen.	r	Eigen.	r
Baccharis pilularis	0.9345	**0.98**	0.3460	0.21
Eriophyllum staechadifolium	−0.3420	**−0.55**	0.8798	**0.82**
Erigeron glaucus	0.0778	0.22	−0.2989	**−0.49**
Scrophularia californica	−0.0077	−0.04	−0.1024	**−0.30**
Anagallis arvensis	−0.0126	**−0.30**	0.0150	0.20

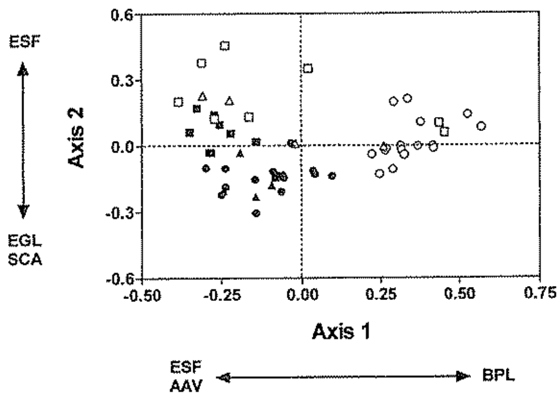

FIG. 3. Ordination of 58 quadrats from Sites 1–3 by principal component analysis along two axes. Black symbols are samples with ≥ 50% canopy gap; white symbols are samples with < 50% gap. Site 1, squares; Site 2, circles; Site 3, triangles. Arrows indicate significant correlations between individual species and axes. BPL = *B. pilularis*; EGL = *E. glaucus*; ESF = *E. staechadifolium*; AAV = *A. arvensis*.

Line transects. Cover of *E. glaucus* increased significantly in 10 m distance classes along transects at Sites 1 and 2 ($P < 0.001$ and $P = 0.012$, respectively; Fig. 5) but was not encountered at Site 3. In contrast, cover of *S. californica* decreased significantly along transects extending away from the cliff edge at Site 2 ($P = 0.01$). *Rubus ursinus* Cham. & Schldl. which was also not encountered at Site 3, decreased significantly away from the cliff edge at Sites 1 and 2 ($P < 0.001$ and $P = 0.027$, respectively). Significantly higher cover near the cliff edge was also detected for *E. staechadifolium* and *A. millefolium* at Site 2 but the spatial patterns were less clear. *Vulpia bromoides* (L.) S.F. Gray was the only species that showed zonation at Site 3, decreasing in abundance at 24 m and farther from the cliff edge.

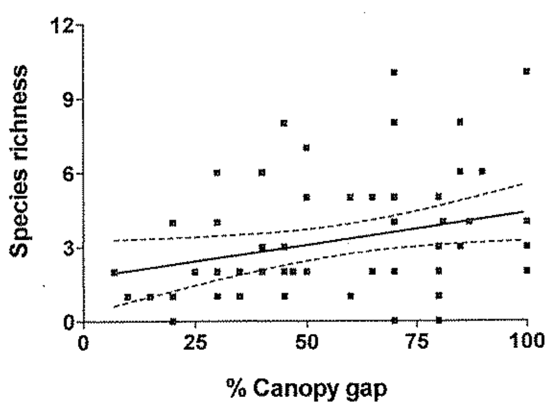

FIG. 4. Regression of species richness versus percent canopy gap for the 58 quadrats sampled. Dashed lines indicate 95% C.I. above and below the least squares fit line ($R^2 = 0.083$; $P = 0.028$).

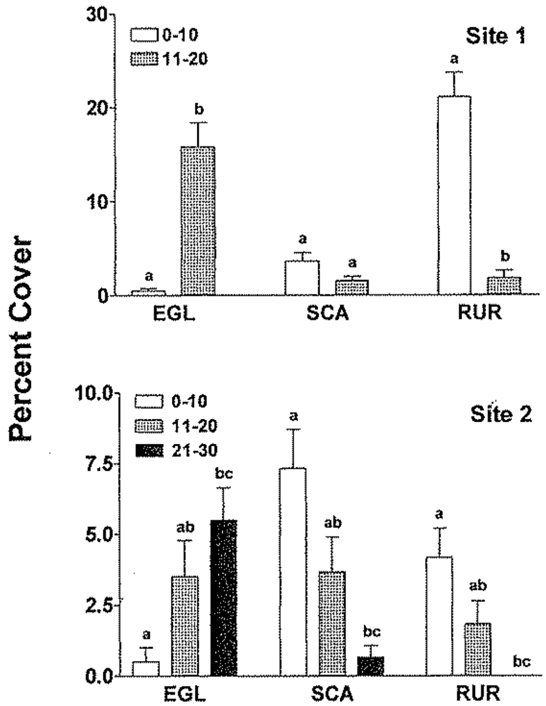

FIG. 5. Comparison of percent cover of *E. glaucus* (EGL), *S. californica* (SCA) and *R. ursinus* (RUR) in 10 m distance classes along transects at Sites 1 and 2. Values are means (±1 SE) of the three transects per site. Lower numbered distance classes are nearest to the cliff edge.

Zonation was also observed for *Baccharis* gaps and Other gaps (Table 6), although it was site-specific. No zonation of *Baccharis* gaps was observed at Sites 1 and 3. However, the extent of *Baccharis* gaps at Site 2 was lower within 20 m of the cliff edge than farther away. Other gaps showed significant zonation at Sites 1 and 3 but the spatial patterns were opposite. At Site 1, the extent of Other gaps in the nearest distance class to the cliff edge was higher than farther away. In contrast, at Site 3 the extent of Other gaps was highest in the farthest distance class from the cliff edge and lowest in the nearest distance class. No zonation was observed for Other gaps at Site 2.

TABLE 6. MEAN PERCENT *BACCHARIS* GAP (BG) AND OTHER GAP (OG) IN 10 M DISTANCE CLASSES ALONG TRANSECTS AT EACH SITE. Column means with different superscript letters are significantly different at $P < 0.05$.

	Sites					
	1		2		3	
Distance class (m)	BG	OG	BG	OG	BG	OG
0–10	42.3[a]	25.0[a]	27.0[a]	3.0[a]	39.5[a]	17.8[a]
11–20	44.5[a]	12.0[b]	35.8[a]	7.7[a]	40.0[a]	23.5[ab]
21–30	—	—	54.5[b]	0.0[a]	29.8[a]	36.5[b]

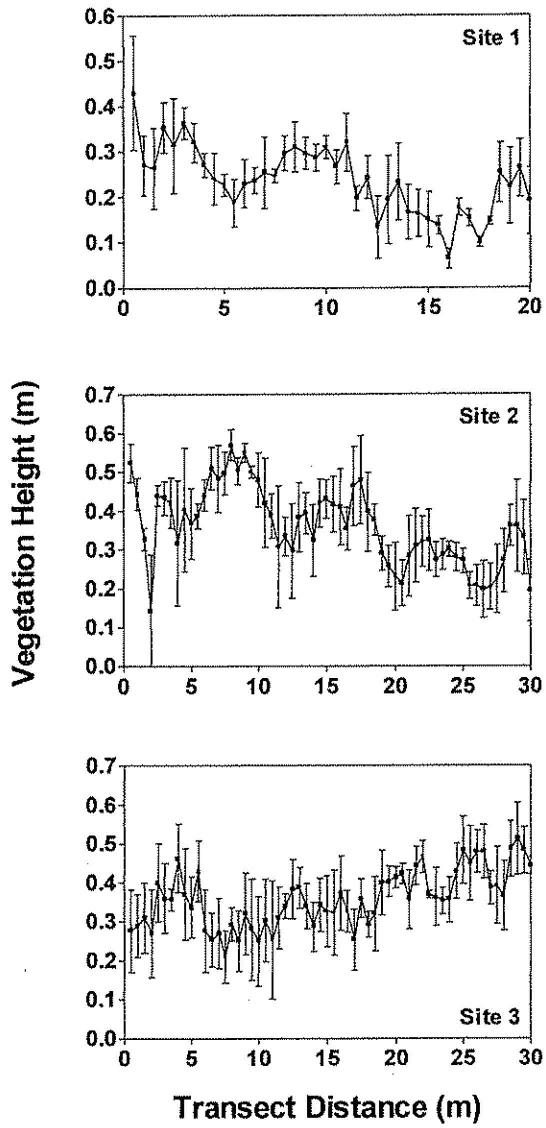

FIG. 6. Mean vegetation height along line transects at each site. Points are means of the three transects per site. Bars indicate ± 1 SE. Note the difference in scale on the x-axis for Site 1.

Mean vegetation height was lower at Site 1 than at Sites 2 or 3 ($P = 0.005$). The latter two sites did not differ from one another. Scrub height decreased with increasing distance from the bluff edge at Sites 1 and 2 ($R^2 = 0.539$, $P < 0.001$ and $R^2 = 0.438$, $P < 0.001$ respectively), but Site 3 showed the reverse pattern ($R^2 = 0.387$, $P < 0.001$) (Fig. 6). Sites 1 and 2 also exhibited a notable sinusoid pattern in vegetation height along transects.

Baccharis *gap samples.* Despite a fair amount of variability in the data, species richness showed a significant positive relationship to *Baccharis* gap area ($R^2 = 0.084$; $P = 0.028$) and a negative relationship to gap height ($R^2 = 0.199$; $P < 0.001$). However, no relationship was observed between species richness and gap distance from the nearest cliff edge. Species richness was highest in *Baccharis* gaps with the greatest light penetration ($P < 0.001$). The most open gaps (class 1) had 7 ± 1.5 species per gap versus 2.7 ± 0.7 in the most densely branched gaps (class 3) (mean ± SE). Gap class 2 had an intermediate number of species per gap (4.5 ± 0.4) and was significantly different than gap class 3 (mean ± SE). Although *Baccharis* gaps with the greatest light penetration were somewhat larger than gaps in class 2, they were not larger than those with the lowest light penetration (class 3).

DISCUSSION

Our results indicate that canopy gaps, zonation, and topography influence the distribution of scrub species on coastal bluffs in this study and that these factors may be important in the maintenance of northern coastal scrub species diversity. Canopy gaps, zonation, and topographic relief appear to be important at two distinct spatial scales. At the scale of an individual bluff (local scale), canopy gaps and zonation were important factors governing species distribution and diversity. At a larger landscape scale, coastal bluff topographic heterogeneity influenced the distribution of species among bluff sites. Differential exposure to wind, sea-salt aerosols, fog, and solar radiation may be important in generating these patterns at both spatial scales.

Local scale patterns. On individual coastal bluffs, canopy gaps and zonation were important in governing northern coastal scrub species distribution and diversity. In particular, canopy gaps had a strong influence on species composition and relative abundance and a large number of rare species occurred exclusively in gap-dominated (≥50% gap) quadrats. We also observed a positive relationship between species richness and percent canopy gap. Zonation was also observed, with the distribution of several species, canopy gaps and vegetation height influenced by bluff position.

Species zonation and vegetation height patterns observed on individual bluffs may be due to differences in soil moisture and the impact of wind and salt spray within bluffs. The importance of wind and salt spray as a constraint on the growth of coastal bluff species is well known (Oosting and Billings 1942; Boyce 1954; Malloch 1972). Barbour (1978) found that small-scale variation in salt spray deposition played an important role in influencing the distribution of northern coastal scrub vegetation at Point Reyes National Seashore. In this study moisture levels nearest the cliff edge may be higher due to stronger winds, decreased evapotranspiration, and greater insulation by taller and denser vegetation near the cliff edge. This could account for the distribution of several species typical of mesic habitats that occurred adjacent to the bluff edge (e.g., *R. ursinus*; Fig. 5). A greater impact of wind—and potentially salt spray—farther inland could also account for the decreased vegetation height observed away from the bluff edge at Sites 1 and 2. Decreased vegetation height away from the cliff edge at Sites 1 and 2 may have influenced zonation of several of the perennial herbs.

Differences in species composition between canopy gaps and scrub vegetation suggest that species responded differently to the contrasting conditions present in these two distinct habitat patches. In this study 38% of species were encountered only in quadrats dominated by canopy gaps compared to 8% in vegetation-dominated samples. Such a large proportion of "gap species" could explain the higher species richness we found in quadrats with higher percent gap. Although it occurred in both gap and scrub vegetation, the rhizomatous species *S. californica* occurred more often in gaps than the surrounding scrub. Indeed, a rhizomatous habit may be advantageous in this vegetation because clonal reproduction would allow for rapid establishment and colonization in newly formed gaps. Such establishment patterns by rhizomatous species have been observed in studies of old-field succession and disturbance (Beckwith 1954; Bazzaz 1979; Sebens and Thorne 1985).

Small spatial scale variation in salt spray deposition (Barbour 1978) and sensitivity to salt spray by the three gap-forming shrubs in this study suggest that sea-salt deposition could be an important factor generating canopy gaps in this vegetation. Holton Jr. and Johnson (1979) observed that the leaves of *B. pilularis* were significantly damaged by salt spray, more so than either *E. staechadifolium* or *L. arboreus*. This might explain why canopy gaps were most prevalent in *B. pilularis* (*Baccharis* gaps were encountered in 93% of samples versus 33% for Other gaps). Localized pockets of differential impact by wind and salt spray could also explain the patchy nature of gaps. Leaf senescence on the windward side of these shrubs and the wind-shaped growth form of the most exposed individuals also suggest that wind and salt spray deposition influence gap formation (Baxter, 1992). Although canopy gaps in *B. pilularis* could be caused by herbivory, it seems unlikely that the pattern of herbivory would mirror that of gaps, and we observed no evidence that this might be the case. Despite circumstantial evidence supporting the role of sea-salt deposition in gap formation, this mechanism needs to be tested in future studies.

Our observation that the smallest *Baccharis* gaps had the highest density of young branches and the largest gaps had few branches and were the most open and decayed suggests that *Baccharis* gaps may enlarge over time. The wide range of gap sizes and branch densities found in this vegetation also suggest that there is a mosaic of canopy gaps of different ages and, therefore, in different stages of succession.

Our results regarding the role of canopy gaps are consistent with a non-equilibrium patch dynamical system mediated by natural disturbance. Non-equilibrium disturbance-mediated dynamics have been proposed elsewhere as a mechanism driving species coexistence and the maintenance of species diversity (Pickett 1980). This mechanism suggests that over the entire community a mosaic of patches of different successional ages exist, all recovering from past disturbances and together providing a wider range of habitats or conditions to which species may become adapted (Grubb 1977; Denslow 1980, 1985). A patchy distribution of resources could also buffer competitive interactions (Chesson and Huntly 1989) or limit the ability of some species to colonize new patches (Tilman 1994). Differential species tolerances and resource requirements are also important in determining species coexistence in heterogeneous environments (Tilman 1982; Keddy 1984).

Consistent with disturbance-mediated gaps in other systems (Levin and Paine 1974), canopy gaps in the scrub vegetation introduce a high degree of structural and resource heterogeneity. For example, light levels in gaps are higher than under the surrounding scrub canopy and, together with low litter inputs, increased solar radiation likely reduces within-gap moisture levels. Soil nutrients may also be less available due to greater soil leaching, low leaf litter inputs and lower rates of nutrient mineralization. However, canopy gaps in northern coastal scrub differ from other disturbance-mediated gaps in that they form over a long period of time and occupy an unusually large cumulative area (45% aerial coverage), which appears to be recolonized slowly.

Landscape patterns. Differences in species composition and abundance among the three coastal bluff sites in this study suggest that topographic relief influences northern coastal scrub species composition and relative abundance. This is consistent with Grams et al. (1977), who suggested that soil moisture, as determined by site exposure, is an important determinant of northern coastal scrub species composition. Although environmental factors were not measured, it is likely that variation in wind, sea-salt deposition, fog, and solar radiation among our topographically distinct bluff sites influenced plant species composition by affecting the moisture regime among sites.

By influencing evapotranspiration rates, and soil water availability, wind and the deposition of sea-salts onto the soil and vegetation can have a strong influence on coastal species, including those in California coastal communities (Barbour 1978; Ogden 1979). Indeed, increased soil salinity levels caused by sea salt deposition were observed to increase plant water stress (Boyce 1954), suggesting lower soil water availability.

Because salt spray deposition increases with increasing wind speed (Malloch 1972), the level of salt spray deposition should vary depending on bluff exposure. Sites exposed to the direct impact of the prevailing winds should receive the highest inputs of sea-salts and show the greatest vegetation response to salt spray deposition. Low mean vegetation height at Site 1 suggests increased wind impact, perhaps in combination with elevated salt spray deposition. Notably, a preliminary assessment of salt spray deposition at the three bluff sites resulted in 8 of 9 filter paper collector strips at Site 1 being torn off of the microscope slides on which they were mounted (no evidence of animal removal was observed). Filter paper strips remained intact at the other two sites. Although this suggests higher wind velocity at Site 1, it could not be determined if higher levels of salt spray were actually deposited at this site.

Differences among bluffs in solar radiation or precipitation via fog drip may also alter soil moisture and influence the distribution of species. For example, *E. staechadifolium,* which was most abundant at Site 3, is often found in mesic habitats (Grams et al. 1977), suggesting that Site 3 may be wetter than Sites 1 or 2. Similarly, the presence at Site 2 of *Artemisia californica* Less. and *Satureja douglasii* (Benth.) Briq., which tend to occur in drier locations (Grams et al. 1977), suggests that this site may be relatively dry.

Although bluff topography may influence the composition and distribution of northern coastal scrub species by affecting the moisture regime of individual escarpments, this appears to occur in a complex way. For instance, the tendency of ocean-facing bluffs to be xeric from direct exposure to prevailing winds and salt deposition may be counteracted by additional input of precipitation via fog drip. In this way fog may act to mediate evapotranspirative moisture loss on exposed sites. Indeed, several species that typically occur in mesic habitats were found at Site 1, which is most exposed to the impacts of wind and salt spray.

In conclusion, canopy gaps, zonation, and topography played an important role in influencing the distribution of northern coastal scrub species on coastal bluffs in this study. As a consequence, these factors may be important in the maintenance of northern coastal scrub species diversity on maritime bluffs. Efforts to preserve this vegetation may be best achieved by maintaining local- and landscape-level heterogeneity through preservation of a range of bluff habitats each varying in extent and topographic relief.

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