ENVIRONMENTAL RELATIONSHIPS OF HERBS IN BLUE OAK (*QUERCUS DOUGLASII*) WOODLANDS OF CENTRAL COASTAL CALIFORNIA

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ABSTRACT

Compositional patterns of herbaceous vegetation and its relationship to environmental factors were investigated in blue oak woodlands and forests in southern San Luis Obispo and northern Santa Barbara counties, California, Based on ordination and classification analyses, herbaceous cover data from 208 0.04-ha plots clustered into three distinct geographic regions. Herbaceous vegetation was strongly associated with overstory crown cover, slope, potential solar insolation and elevation. A-horizon coarse fragment was a significant variable in two regions and available water capacity was important in one region.

Blue oak (*Quercus douglasii* H. & A.) woodland is the dominant hardwood type in California covering over one million hectares. Although blue oak co-occurs with other tree species, it typically covers extensive areas in monospecific stands. The blue oak series is composed of at least twelve different subseries, four of which have a relatively high cover of understory shrubs (Allen et al. 1990). For the most prevalent subseries, however, the shrub component is insignificant compared to the ubiquitous herbaceous understory dominated by annual forbs and grasses.

Because blue oak woodland provides 65% of the state's livestock forage (Bartolome 1987), research on understory herbaceous vegetation has focused on the effects of overstory removal on forage production (Murphy and Crampton 1964; Murphy and Berry 1973; Kay 1987), differences in forage production and species composition between oak canopies and adjacent open grassland (Holland 1980; Frost and McDougald 1989; McClaran and Bartolome 1989), and responses of a relatively limited number of species, e.g., *Avena* spp., *Bromus* spp., *Vulpia* spp. and *Erodium* spp. to different grazing regimes (Rosiere 1987). Holland (1973) and Callaway (1990) have studied the influence of the canopy on ungrazed herbaceous cover.

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We know of no studies, however, that have examined variation in blue oak understory vegetation on a regional scale in relation to environmental factors. In this paper we describe quantitative relationships between herbaceous composition and environmental factors for blue oak woodlands and forests in the southern end of its range. Classification and management of these ecosystems will be presented in a subsequent paper.

Sites and Methods

Study area. The study area included 8 7.5′-topographic quadrangles and was a patchwork of blue oak woodland and forest in southern San Luis Obispo and northern Santa Barbara counties at the juncture of three mountain ranges: the La Panza Range, Garcia Mountain, and the Sierra Madre Mountains (Fig. 1). The center of the study area (35°10′N, 122°10′W) was located approximately 52 km ESE of San Luis Obispo. Climate is mediterranean with cool wet winters and warm dry summers. Most precipitation falls between November and March. Average annual precipitation declines rapidly from west to east. For the relatively more coastal stations of Pozo and Pine Canyon average annual precipitation is 526 mm and 450 mm, respectively. In contrast, average annual precipitation at La Panza Ranch east of the La Panza Range is 223 mm and at Cuyama east of the Sierra Madre Mountains it is 163 mm. We sampled the vegetation over a four year period from 1986–1989. Precipitation at Pozo was 713 mm in 1986, higher than the average, but below average in the remaining years: 269, 453, and 328 mm in 1987, 1988, and 1989, respectively.

Basement rock of the area is granite and Franciscan sandstone overlain by early Tertiary sedimentary rocks composed of marine sandstone, shale, and conglomerates (Dibblee 1976). Soils in the area are variable but most are mollisols, primarily argixerolls and haploxerolls.

The ten allotments within the study area have been grazed almost continuously by cattle since 1900. Grazing regimes of the allotments have been highly variable historically. Currently four allotments are grazed year around and the others are grazed from one to five months. None of the plots had burned within a period of 5 years before the study.

Sampling methods. Plot data were collected from the study area over a period of four years from late March to late May. In 1986 and 1987, 77 plots were sampled in the area from Pozo to Cuyama River west of Branch Mountain (Fig. 1). Five of these, representing a spectrum of environments, were revisited in 1987. In 1987, 53 plots were sampled in the area from Cuyama River to Miranda Pine

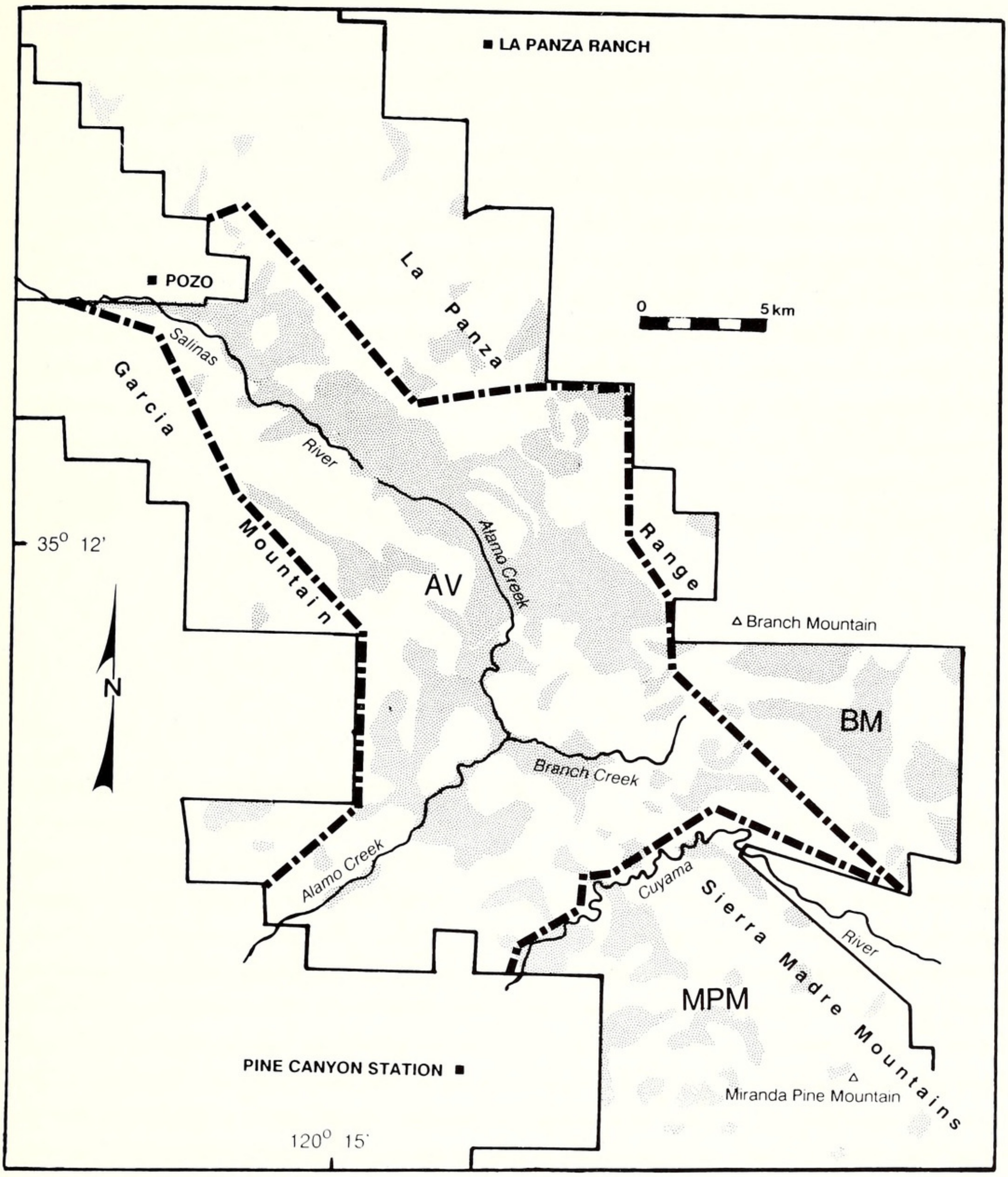

FIG. 1. Map of the study area. Shaded areas are oak woodland and forest. Herbaceous vegetation regions indicated by the dot-dashed lines are: Avenales (AV), Miranda Pine Mountain (MPM) and Branch Mountain (BM). Solid line is the boundary of Los Padres National Forest.

Mountain, four of which were revisited in 1989. In 1988, 78 plots were sampled in the area east of Branch Mountain, six of which had been sampled in 1987.

Plots of four hundred square meters were subjectively located in stands where blue oak overstory crown cover attained at least 20 percent and understory herbaceous cover exceeded 60 percent. A stand was sampled if oaks were relatively evenly distributed over the plot on the same slope and aspect.

Slope angle, aspect, elevation, landform, slope position, and within-plot vertical and horizontal microrelief were recorded for each plot. Slope and aspect were used to obtain an estimate of potential annual solar insolation (solar insolation) using the tables of Frank and Lee (1966).

Percentage foliar cover of all plant species was estimated visually and recorded into a modified Braun-Blanquet cover scale: 0–1%, 2–5%, 6–25%, 26–50%, 51–75%, and 76–100%. Midpoints of each of these cover classes were used in data analysis. The cover of overstory trees was measured with a spherical densiometer (Lemmon 1956) by averaging five values taken in the plot: one at plot center and the others 7.5 m parallel and perpendicular to the slope contour from plot center. Trees larger than 5 cm dbh were counted and their diameters measured at 1.4 m.

A soil pit was excavated in each plot to a depth of 100 cm or bedrock, whichever was encountered first. Thickness of the A horizon was measured and its color, texture, and pH noted. The same parameters also were taken for the subsoil. In addition, percentage coarse fragment content was estimated for each layer. Soil drainage, rootability, and lithology were recorded. Available water capacity (AWC) was calculated for the top 50 cm of soil where most herbaceous species were rooted.

Data analysis. We analyzed herbaceous species cover data using two-way indicator species analysis (TWINSPAN) (Hill 1979), detrended correspondence analysis (DCA) (Hill and Gauch 1980), and canonical correspondence analysis (CCA) (Ter Braak 1986). Only herbaceous species were analyzed because they are most similar in their ecological requirements. TWINSPAN, a polythetic divisive classification technique, was used to elucidate regional variation in understory vegetation. Detrended correspondence analysis (DCA) was then utilized to examine compositional variation and overlap of the TWINSPAN groups; it is ordination method that portrays the relative similarity of samples along a few principal axes of variation. Also, DCA was used to compare changes in the positions of the 15 resampled plots in the ordination space. Canonical correspondence analysis (CCA) was used to examine species–environment relationships for each of the regions identified using two-way indicator species analysis (TWINSPAN) and detrended correspondence analysis (DCA). Canonical correspondence analysis (CCA) is designed to detect unimodal relationships between species and external variables by performing a constrained correspondence analysis ordination; that is, the ordination axes extracted by this method are required to be a linear combination of environmental variables. Axes appear in order of the variance explained.

Continuous variables used in the CCA analysis included elevation, aspect, slope, solar insolation, tree density, overstory crown cover, A-horizon coarse fragment content, subsoil coarse fragment content, and available water capacity of the soil. Soil pH showed little variability and was not used. If necessary, continuous variables first were normalized and then standardized to a mean of 0 and standard deviation of 1. Categorical variables used in the analysis included slope position, within-plot horizontal and vertical microrelief, and A-horizon surface texture.

Rare species were downweighted by reducing species abundance values in proportion to their frequencies of occurrence, for species with frequencies less than 20% of the most frequent species. Nomenclature follows Hoover (1970).

Results

Based on TWINSPAN and DCA results we recognized three vegetation groups associated with three distinct geographic regions, referred to as Avenales, Miranda Pine Mountain and Branch Mountain (Figs. 1 and 2). The Cuyama River separates the Avenales and Miranda Pine Mountain regions and the boundary between the Branch Mountain and Avenales regions follows the north–south trending chaparral-covered ridge west of Branch Mountain. Compositional differences among the regions were both the result of differences in species composition (Table 1) and changes in species cover. The first DCA axis was correlated with overstory crown cover ($r = 0.40$, $P < 0.001$) and the second axis was correlated with solar insolation ($r = -0.69$, $P < 0.001$) and slope ($r = 0.44$, $P < 0.001$).

Plot ordination scores were not very sensitive to sampling year; that is, resampled plots remained within the same region in the DCA ordination space (Fig. 2). Moreover, when the 15 resampled plots were combined with the 208 plots in a TWINSPAN analysis, they remained in the same regions of the ordination (Fig. 2). Interannual differences in plot ordination scores were influenced primarily by the presence or absence of species with less than 1% cover rather than by marked fluctuations in the cover of dominant species.

In the analysis of Avenales 163 species entered the CCA. For Avenales samples, slope, overstory crown cover and solar insolation are correlated with the first canonical axis (Table 2). A-horizon coarse fragment is correlated with the second axis and elevation is correlated with the third axis. Inspection of bivariate scattergrams of canonical scores vs. environmental variables revealed that seven plots with overstory crown cover of less than 50% strongly influenced the CCA results and produced the strong relationship of CCA with overstory crown cover (Fig. 3). After removing these plots, overstory crown cover was not related to CCA axes. The contributions of slope and solar insolation remained the same. The coefficients for eleva-

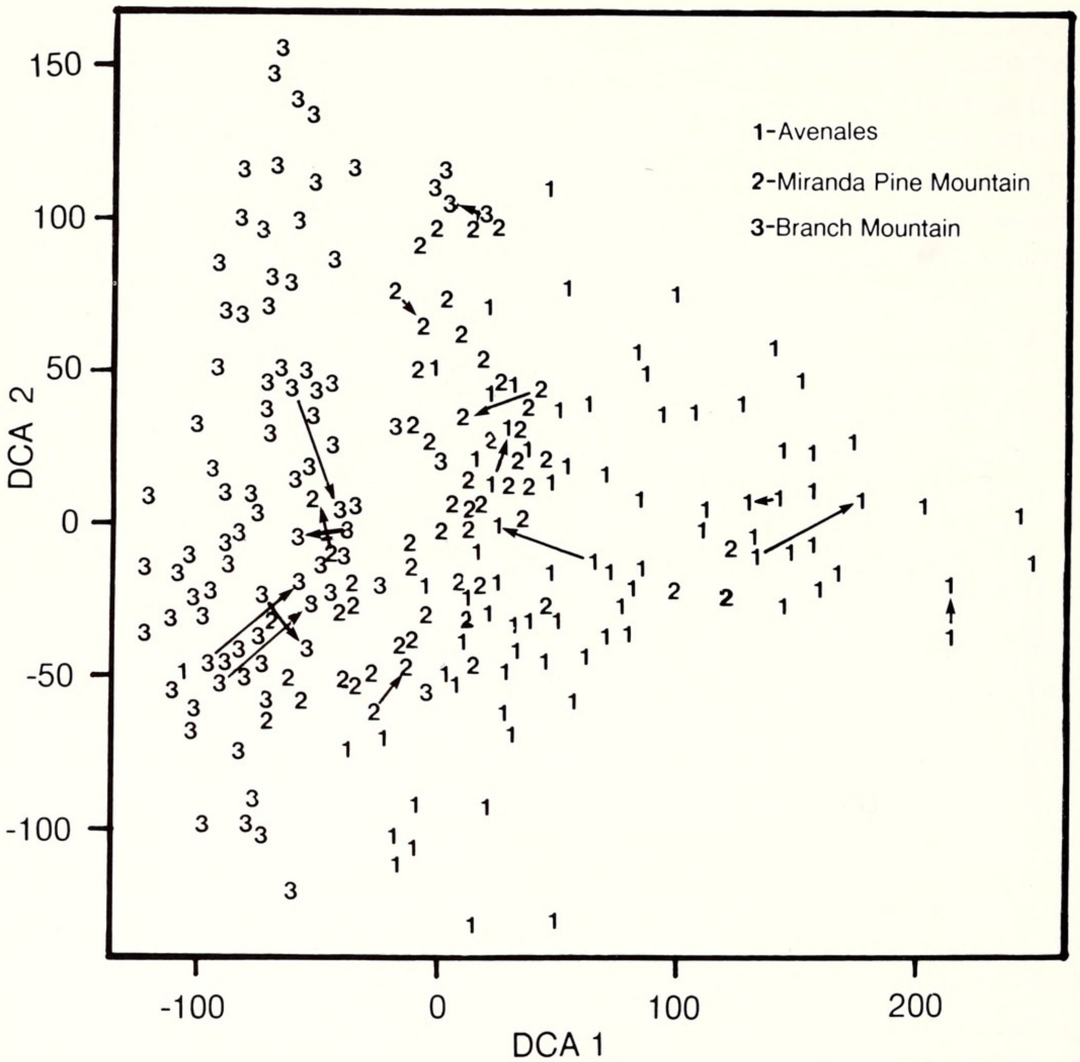

FIG. 2. Detrended correspondence analysis (DCA) ordination of the 208 plots. Arrows show the trajectories of compositional change for the 15 plots visited for two years. Axis 1 is correlated with overstory crown cover (r = 0.40) and axis 2 is correlated with solar insolation (r = −0.69) and slope (r = 0.44).

tion and A-horizon coarse fragment changed in magnitude but not direction (Table 3).

Arrow length in the canonical correspondence analysis (CCA) ordination diagram (Fig. 4) is proportional to the strength of the correlation between environmental variable and ordination axes. Arrow direction indicates whether a variable is positively or negatively related to the axis. A species point projected perpendicularly onto each environmental axis corresponds approximately to the ranking of the weighted average of the species with respect to that environmental variable. The weighted averages are approximated in the diagram as deviations from the grand mean of each variable. The origin of the plot represents the grand mean. Table 4 presents the means of variables shown in the CCA ordination diagrams. The

TABLE 1. SPECIES CONCENTRATED IN A PARTICULAR REGION. Values are percentage of plots in a region in which a species is present.

	Avenales	Miranda Pine Mountain	Branch Mountain
Agoseris grandiflora	28	1	7
Avena fatua	66	22	9
Bromus carinatus	20	3	1
Euphorbia spathulata	43	6	1
Lotus micranthus	12	—	—
Lotus purshianus	11	—	—
Lotus strigosus	4	—	—
Lupinus nannus	8	—	—
Medicago polymorpha	65	23	1
Microseris elegans	4	—	—
Nemophila pedunculata	19	—	—
Ranunculus californicus	34	—	—
Sisyrinchium bellum	25	—	—
Sonchus oleraceus	8	—	—
Torilis nodosa	15	—	—
Trifolium bifidum	29	—	—
Vicia americana	6	—	—
Vicia exigua	14	—	—
Vicia sativa	8	—	—
Athysanus pusillus	—	30	54
Calochortus venustus	—	13	—
Gilia achilleaefolia	—	4	—
Monardella villosa	—	5	—
Phacelia imbricata	—	6	—
Sitanion hystrix	—	4	—
Stellaria nitens	—	11	—
Stipa cernua	—	13	—
Alchemilla occidentalis	5	—	36
Androsace acuta	—	3	33
Arenaria douglasii	—	—	14
Astragalus antisellii	—	—	9
Bromus rubens	16	39	77
Capsella bursa-pastoris	3	11	26
Filago gallica	—	—	8
Lactuca serriola	5	3	27
Lagophylla ramosissima	—	12	47
Lasthenia chrysostoma	2	1	33
Linanthus androsaceus	—	—	13
Lithophragma affine	—	—	9
Lupinus subvexus	—	—	58
Navarretia mitracarpa	—	—	28
Plagiobothrys tenellus	—	—	10
Polypogon monspeliensis	—	—	10
Rigiopappus leptocladus	—	—	37
Tropidocarpum gracile	—	—	12

TABLE 2. CANONICAL COEFFICIENTS AND INTRASET CORRELATIONS OF THE CANONICAL CORRESPONDENCE ANALYSIS FOR UNDERSTORY HERBACEOUS SPECIES DATA FROM THE AVENALES REGION, N = 77. The first three axes explain 89% of the variance in the weighted average of the species with respect to the environmental variables. Only variables with correlation coefficients greater than 0.40 on one of the first three axes are shown. Canonical correspondence analysis canonical coefficients are the regression coefficients used to derive axes from a linear combination of the standardized environmental variables. Intraset correlations are the correlations among the standardized environmental variables and the canonical correspondence analysis axes.

	Canonical coefficients			Correlation coefficients		
Axis variable	1	2	3	1	2	3
Solar insolation	−0.27	0.28	0.05	−0.71	0.36	0.07
Overstory cover	0.15	−0.02	−0.09	0.62	0.05	−0.16
Slope	0.18	0.02	0.19	0.58	0.31	0.32
A-horizon coarse fragment	−0.10	−0.24	0.11	−0.35	−0.41	0.43
Elevation	0.05	0.02	0.22	0.06	−0.14	0.60

pattern of species points in Figure 4 indicates that they are fairly equally distributed between environments on steep slopes with low solar insolation (upper right quadrant) and gentle slopes with high solar insolation (upper left quadrant). Furthermore, species tend to be more prevalent on soils with lower A-horizon coarse fragments, e.g., *Bromus arenarius. Trifolium tridentatum,* in contrast, occurs on soils with high coarse fragment content.

Because of the large number of species in the analysis, we selected 12 species (6 native and 6 introduced) that were present in all the regions to make the diagrams more readily interpretable. To demonstrate the relationship between the ranking of a species on an environmental variable in the CCA ordination diagrams and the actual values of a species for a variable, we present median solar insolation values for 8 species and the median solar insolation value

TABLE 3. CANONICAL COEFFICIENTS AND INTRASET CORRELATIONS OF THE CANONICAL CORRESPONDENCE ANALYSIS FOR UNDERSTORY HERBACEOUS SPECIES DATA FROM THE AVENALES REGION AFTER REMOVING PLOTS WITH LESS THAN 50% OVERSTORY CROWN COVER, N = 70. Only variables with correlation coefficients greater than 0.40 on one of the first three axes are shown. The first three axes accounted for 78% of the variance in the weighted average of the species with respect to the environmental variables.

	Canonical coefficients			Correlation coefficients		
Axis variable	1	2	3	1	2	3
Slope	0.25	0.21	0.14	0.66	0.30	0.19
Solar insolation	−0.23	0.21	0.20	−0.64	0.29	0.36
A-horizon coarse fragment	−0.02	−0.27	0.06	−0.00	−0.57	0.36
Elevation	0.08	−0.03	−0.19	0.24	−0.28	0.54

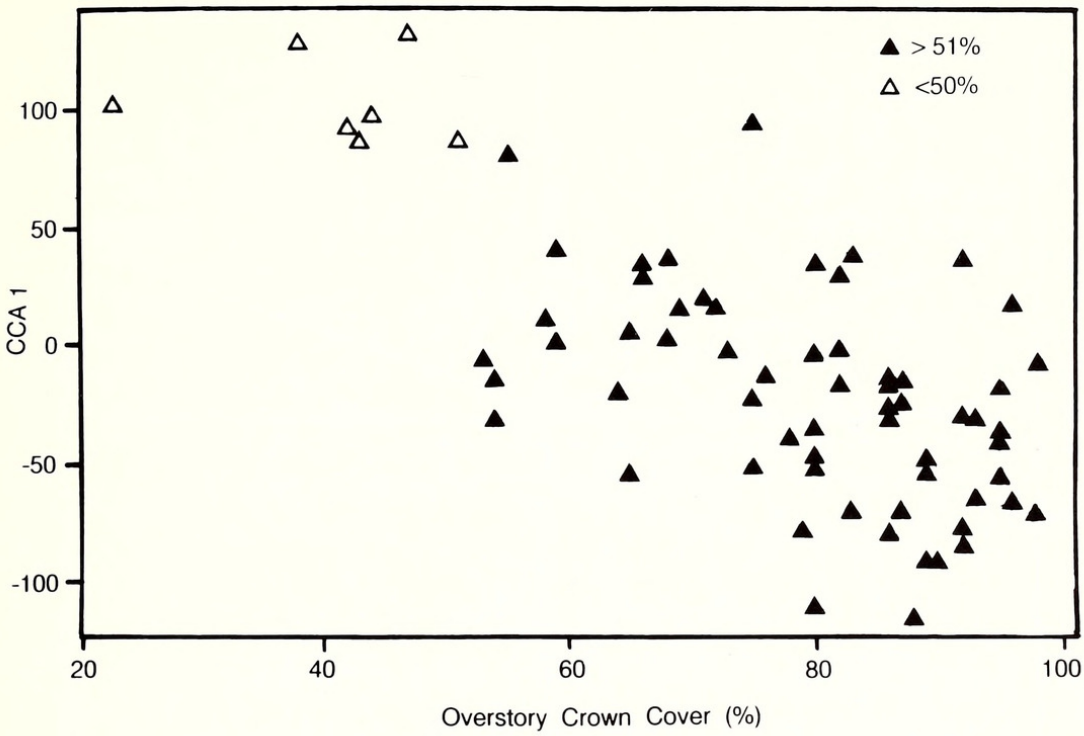

FIG. 3. Canonical correspondence analysis (CCA) first-axis scores plotted against overstory crown cover for the 77 Avenales plots. Plots with cover of less than 50% are indicated by open triangles.

for all the plots in a region (Fig. 5). Median solar insolation values were calculated for plots in which the species cover was at least 5%. We did not include plots with less than 5% cover because chance occurrences are more likely in this cover interval. Such occurrences could distort median values and the overall pattern.

In Avenales (Fig. 5a) median values for *Sanicula bipinnata, Claytonia perfoliata* and *Bromus madratensis* are below the median value for all the plots, *Bromus diandrus* and *Avena barbata* near the all-

TABLE 4. MEANS OF ENVIRONMENTAL VARIABLES SHOWN IN THE CANONICAL CORRESPONDENCE ANALYSIS ORDINATION DIAGRAMS. A one-way analysis of variance indicated only available water capacity was significantly different ($P < 0.05$) among the regions.

Variable	Avenales	Miranda Pine Mountain	Branch Mountain
Elevation (m)	746	723	728
Slope (degrees)	21	18	18
Potential annual solar insolation (kg calories cm^{-2} yr^{-1})	232	232	252
A-horizon coarse fragment (%)	7	8	12
Available water capacity (cm^3 of water 50–cm^{-3} soil)	0.97	0.84	0.68

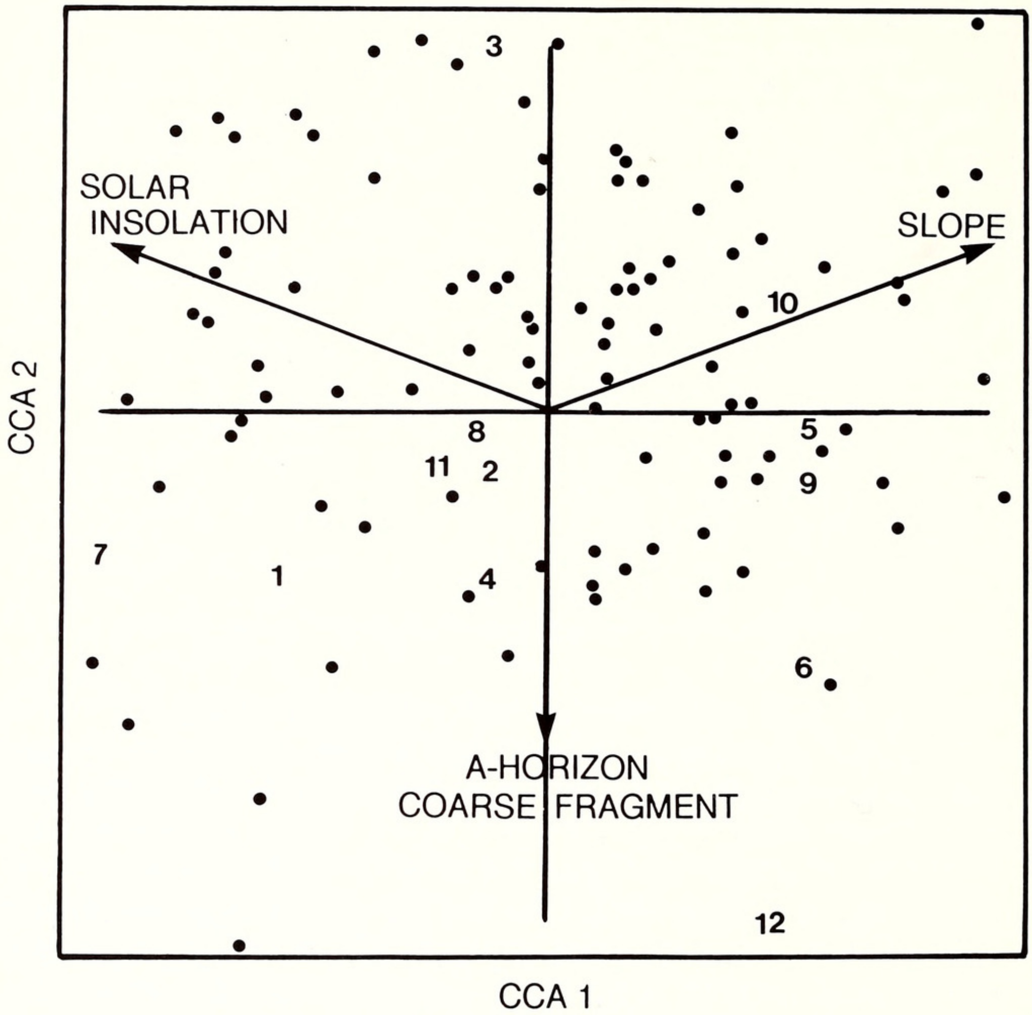

FIG. 4. Canonical correspondence analysis (CCA) ordination diagram with species and environmental variables (arrows) for the 70 Avenales plots. Dots indicate positions of species with at least 20% frequency in the plots. Species are as follows: 1 *Amsinkia intermedia,* 2 *Avena barbata,* 3 *Bromus arenarius,* 4 *Bromus diandrus,* 5 *Bromus madritensis,* 6 *Claytonia perfoliata,* 7 *Erodium moschatum,* 8 *Lupinus bicolor,* 9 *Madia gracilis,* 10 *Sanicula bipinnata,* 11 *Stellaria media,* and 12 *Trifolium tridentatum.*

plot median and *Bromus arenarius, Lupinus bicolor,* and *Amsinkia intermedia* above the all-plot median. Because CCA scores are based on all plots, species ranking on the solar insolation variable in the diagram (Fig. 4) does not correspond exactly to the ordering of the median values (Fig. 5a). However, the species are correctly located in Figure 4 relative to the origin (grand mean of the variable), indicating that, although the variability in solar insolation is high (Fig. 5a) for each species, CCA accurately retrieves the species–environmental gradient.

Results of the canonical correspondence analysis (CCA) for the 53 Miranda Pine Mountain plots are presented in Table 5. In this region there were 165 species. Slope, overstory cover and solar in-

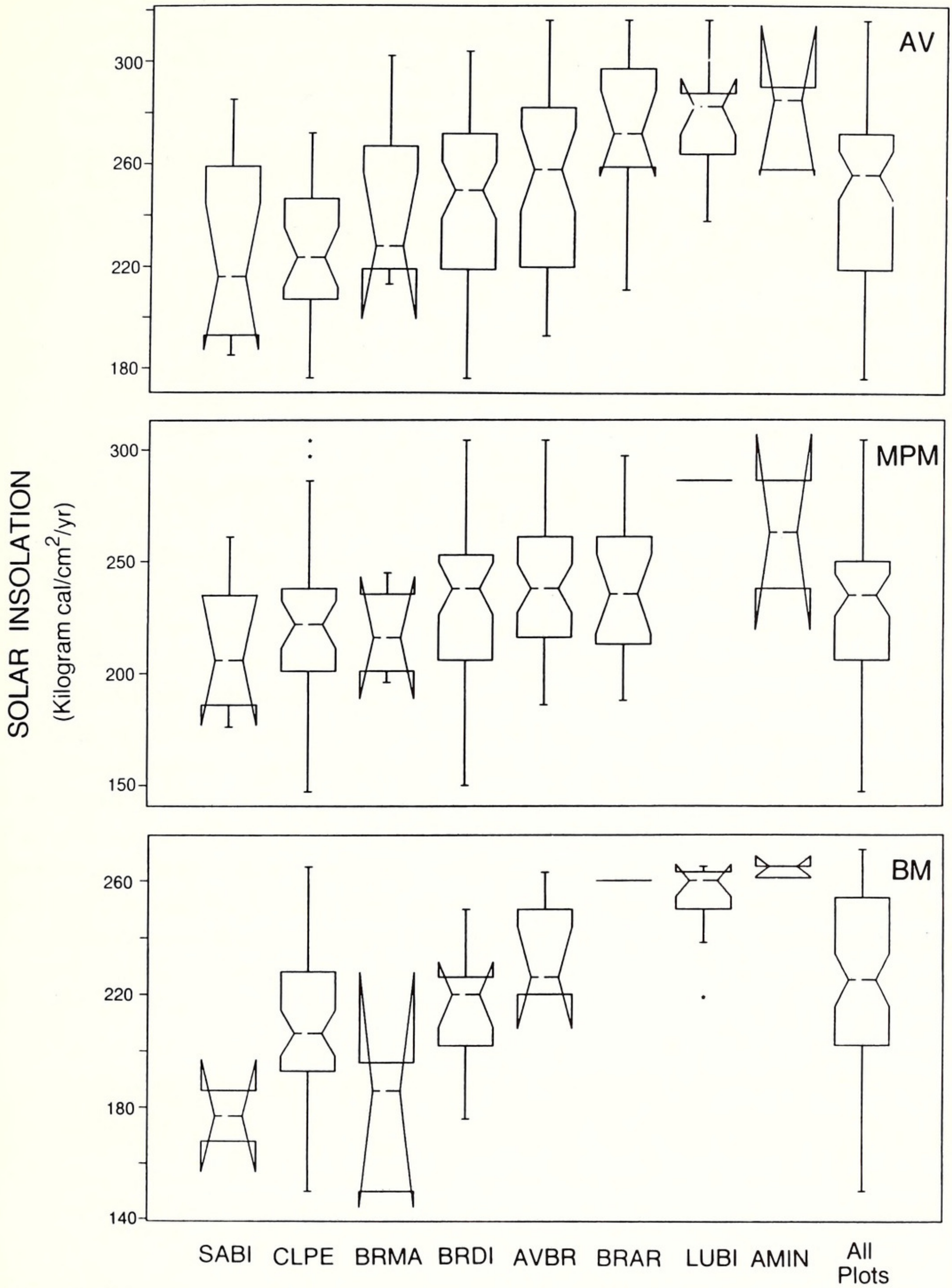

FIG. 5. Solar insolation values for *Sanicula bipinnata* (SABI), *Claytonia perfoliata* (CLPE), *Bromus madritensis* (BRMA), *Bromus diandrus* (BRDI), *Avena barbata* (AVBR), *Bromus arenarius* (BRAR), *Lupinus bicolor* (LUBI), *Amsinkia intermedia* (AMIN) and all the plots in (a) Avenales (AV), (b) Miranda Pine Mountain (MPM) and (c) Branch Mountain (BM). Fifty percent of the observations are within the upper and lower horizontal lines. Vertical lines show the range of values; asterisks are outliers, Non-overlapping of notches among boxes indicates significant differences between distributions at roughly 95% significance level. Reversals occur where the confidence interval exceeds the quartiles.

TABLE 5. CANONICAL COEFFICIENTS AND INTRASET CORRELATIONS OF THE CANONICAL CORRESPONDENCE ANALYSIS FOR UNDERSTORY HERBACEOUS SPECIES DATA FROM THE MIRANDA PINE MOUNTAIN REGION, N = 53. Only variables with correlation coefficients greater than 0.40 on one of the first three axes are shown. The first three axes explain 78% of the variance in the weighted average of the species with respect to the environmental variables.

	Canonical coefficients			Correlation coefficients		
Axis variable	1	2	3	1	2	3
Slope	−0.36	−0.04	−0.24	−0.77	−0.02	−0.31
Solar insolation	0.12	−0.05	−0.20	0.64	−0.28	−0.27
Overstory cover	−0.08	0.00	0.04	−0.41	0.35	0.27
Elevation	−0.11	−0.28	0.15	−0.21	−0.81	0.23
Tree density	−0.10	0.13	0.16	−0.38	0.53	0.35

solation are correlated with the first canonical axis while the second axis is correlated with elevation and density. After the removal of 11 plots with overstory crown cover of less than 50% and one sample with an unusually high A-horizon coarse fragment content, three variables remained: elevation, slope, and solar insolation (Table 6). Nevertheless, correlation coefficients for these variables changed little from the analysis with 53 plots. The CCA ordination diagram for variables in Table 6 is shown in Figure 6. Most species are concentrated at lower elevations, on steeper slopes with low solar insolation values. A comparison of solar insolation values for species in Figure 5b with their ranking and position relative to the origin in the CCA ordination diagram (Fig. 6) indicates a poorer fit. For example, species with high median solar insolation values like *Amsinkia intermedia* and *Lupinus bicolor* are placed near the mean and in the low solar insolation portion of the diagram, respectively. In addition, *Bromus arenarius* should be closer to the origin based on its median value.

TABLE 6. CANONICAL COEFFICIENTS AND INTRASET CORRELATIONS OF THE CANONICAL CORRESPONDENCE ANALYSIS FOR UNDERSTORY HERBACEOUS SPECIES DATA FROM THE MIRANDA PINE MOUNTAIN REGION AFTER REMOVING PLOTS WITH LESS THAN 50% OVERSTORY CROWN COVER, N = 42. Only variables with correlation coefficients greater than 0.40 on one of the first three axes are shown. The first three axes accounted for 74% of the variance in the weighted average of the species with respect to the environmental variables.

	Canonical coefficients			Correlation coefficients		
Axis variable	1	2	3	1	2	3
Slope	0.38	−0.09	0.17	0.76	−0.08	0.23
Solar insolation	−0.12	−0.06	0.26	−0.63	−0.08	0.47
Elevation	0.02	−0.32	−0.02	−0.10	−0.84	−0.11

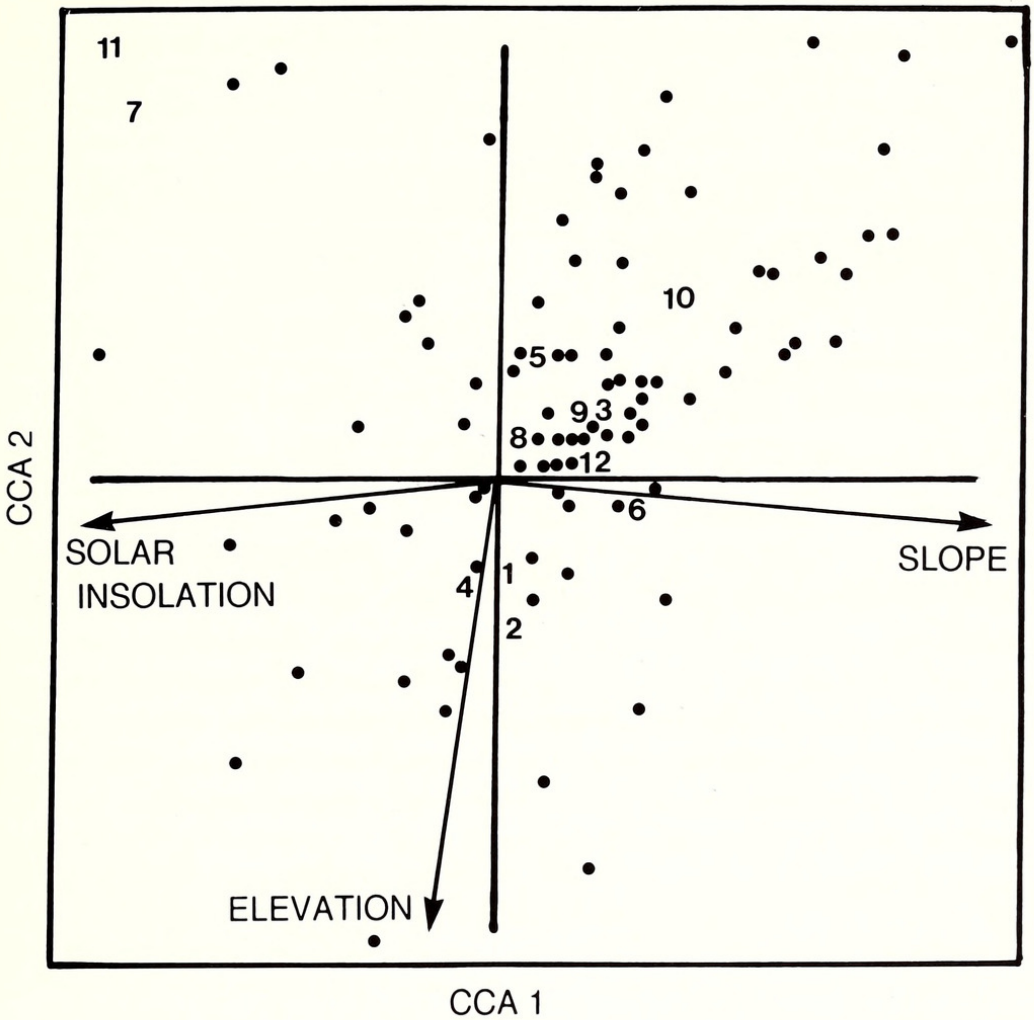

FIG. 6. Canonical correspondence analysis (CCA) ordination diagram with species (O) and environmental variables (arrows) for the 42 Miranda Pine Mountain plots. Species are as follows: 1 *Amsinkia intermedia*, 2 *Avena barbata*, 3 *Bromus arenarius*, 4 *Bromus diandrus*, 5 *Bromus madritensis*, 6 *Claytonia perfoliata*, 7 *Erodium moschatum*, 8 *Lupinus bicolor*, 9 *Madia gracilis*, 10 *Sanicula bipinnata*, 11 *Stellaria media*, and 12, *Trifolium tridentatum*.

One hundred and sixty-one species were analyzed for Branch Mountain. Results of the canonical correspondence analysis (CCA) for the 78 Branch Mountain plots are presented in Table 7. Overstory crown cover, elevation and solar insolation are correlated with the first axis. Available water capacity and elevation are correlated with the second axis. Slope is correlated with the third axis. After 10 plots with overstory crown cover of less than 40% were deleted, the number of variables remained the same but overstory crown cover (Table 7) was replaced by A-horizon coarse fragment which is correlated with the first axis (Table 8). Slope changed from a negative correlation with the third axis to a positive correlation with the first axis. Axis correlations for elevation and solar insolation were little changed by plot deletions.

TABLE 7. CANONICAL COEFFICIENTS AND INTRASET CORRELATIONS OF THE CANONICAL CORRESPONDENCE ANALYSIS FOR UNDERSTORY HERBACEOUS SPECIES DATA FROM THE BRANCH MOUNTAIN REGION, N = 78. Only variables with correlation coefficients greater than 0.40 on one of the first three axes are shown. The first three axes explain 86% of the variance in the weighted average of the species with respect to the environmental variables.

	Canonical coefficients			Correlation coefficients		
Axis variable	1	2	3	1	2	3
Solar insolation	−0.42	−0.23	−0.15	−0.75	0.33	−0.19
Elevation	0.15	−0.40	−0.08	0.52	−0.59	0.01
Overstory cover	0.13	0.11	0.19	0.43	0.10	0.35
Available water capacity	−0.06	0.09	0.00	−0.19	0.41	−0.18
Slope	−0.04	−0.06	−0.32	0.38	0.30	−0.55

The CCA ordination diagram for the results of Table 8 are shown in Figure 7. A greater number of species occur at lower elevations, but otherwise they are equally distributed between the environments with gentle slopes and high solar insolation and steeper, lower solar insolation slopes. In general, the species median solar insolation values (Fig. 5c) correspond well to their placement on the solar insolation gradient in Figure 7.

DISCUSSION

Within this small portion of the range of blue oak there is considerable variability in herbaceous vegetation. When all plots for each region were analyzed, compositional patterns are clearly influenced by overstory crown cover, solar insolation and slope but significant vegetation changes also coincide with major geographic fea-

TABLE 8. CANONICAL COEFFICIENTS AND INTRASET CORRELATIONS OF THE CANONICAL CORRESPONDENCE ANALYSIS FOR UNDERSTORY HERBACEOUS SPECIES DATA FROM THE BRANCH MOUNTAIN REGION AFTER REMOVING PLOTS WITH LESS THAN 40% OVERSTORY CROWN COVER, N = 68. Only variables with correlation coefficients greater than 0.40 on one of the first three axes are shown. The first three axes accounted for 83% of the variance in the weighted average of the species with respect to the environmental variables.

	Canonical coefficients			Correlation coefficients		
Axis variable	1	2	3	1	2	3
Solar insolation	−0.38	−0.24	0.20	−0.72	−0.42	−0.10
Elevation	0.19	−0.37	0.10	0.59	−0.55	0.11
Slope	−0.01	−0.02	0.28	0.46	0.41	0.37
A-horizon coarse fragment	0.10	0.20	−0.08	0.42	−0.12	−0.15
Available water capacity	−0.08	0.07	−0.00	−0.18	0.45	0.04

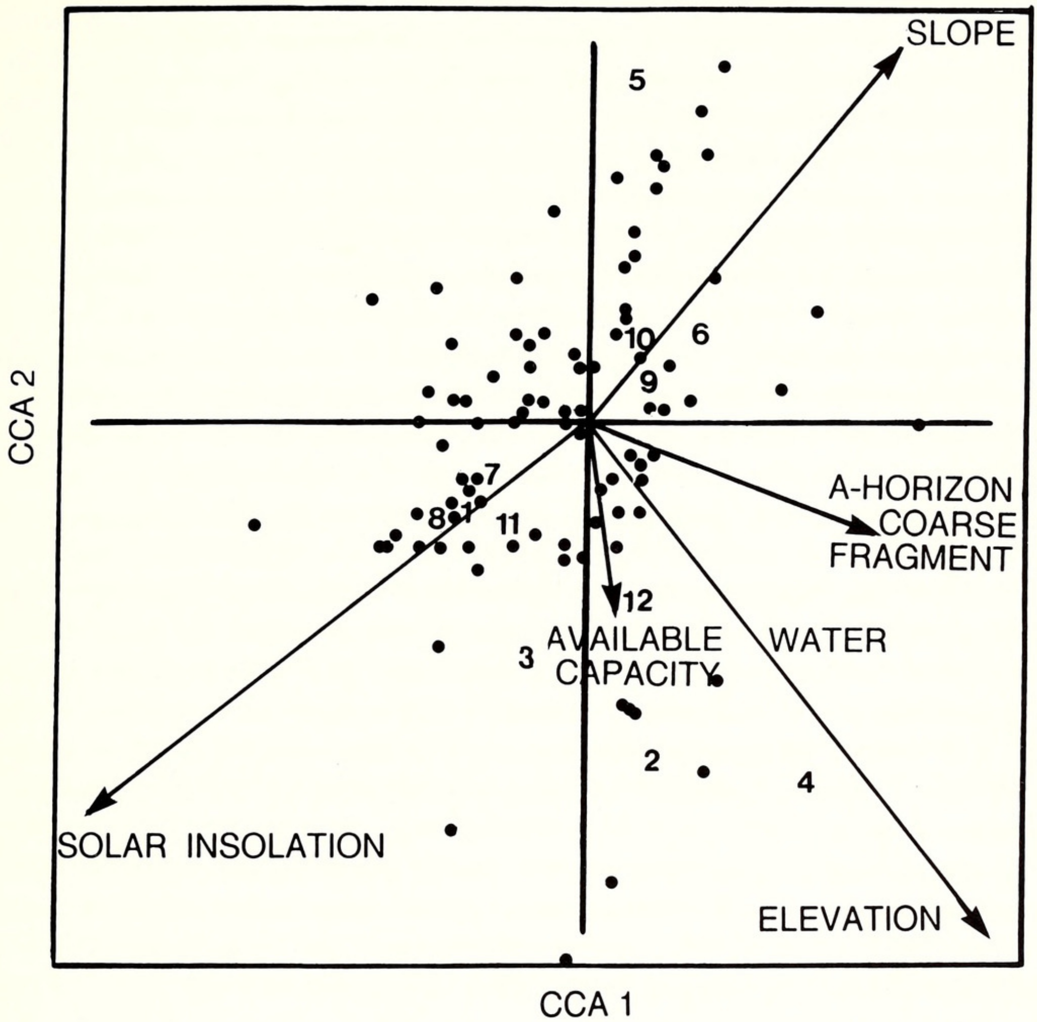

FIG. 7. Canonical correspondence analysis (CCA) ordination diagram with species (O) and environmental variables (arrows) for the 68 Branch Mountain plots. Species are as follows: 1 *Amsinkia intermedia*, 2 *Avena barbata*, 3 *Bromus arenarius*, 4 *Bromus diandrus*, 5 *Bromus madritensis*, 6 *Claytonia perfoliata*, 7 *Erodium moschatum*, 8 *Lupinus bicolor*, 9 *Madia gracilis*, 10 *Sanicula bipinnata*, 11 *Stellaria media*, and 12 *Trifolium tridentatum*.

tures of the study area. Factors responsible for these discontinuities appear complex. Although the first axis of the detrended correspondence analysis (DCA) for the 208 plots is broadly related to overstory crown cover, the ordering of the regions on this axis also suggests the influence of the steep coastal to inland precipitation and temperature gradient. Precipitation stations suggest that Avenales has relatively higher annual precipitation than the other two regions. Additionally, Avenales experiences an ameliorating maritime fog influence during much of the year. Fog is less frequent in the more arid inland regions. Drier inland conditions may explain the importance of elevation as a variable for Miranda Pine Mountain and Branch Mountain since precipitation is correlated with elevation. Livestock grazing also can have a marked effect on regional oak herbaceous vegetation as demonstrated for *Quercus garrayana* woodland (Smith 1985). Unfortunately, grazing regimes in the study area and within each region are highly variable and historic use records are too incomplete to evaluate directly the impact of grazing on the vegetation. Nevertheless, grazing may reinforce climatically-determined vegetation patterns.

Overstory crown cover was consistently an important variable in each region, an expected finding since numerous studies have demonstrated the effect of individual oaks on the composition of herbaceous vegetation. The results, however, show a nonlinear relationship between canopy cover and vegetation change. Composition showed a threshold change when canopy cover increased to 40–50% (Fig. 3) but for higher canopy cover the change was much less pronounced.

Slope and solar insolation also assumed a prominent role in controlling herbaceous vegetation. In temperate latitudes aspect differences in the duration and intensity of solar beam radiation have a dramatic effect on air and soil temperatures and atmospheric and soil moisture (Holland and Steyn 1975; Evans and Young 1989) which in turn influence the vegetation. McNaughton (1968) observed consistent changes in composition and biomass in relation to aspect in ungrazed California annual grasslands on sandstone and serpentine. Similarly, Borchert et al. (1989) noted a solar insolation-related influence on herbaceous composition within a several hectare blue oak forest. The relationship of the vegetation to solar insolation is likely even stronger than reported here because potential annual solar insolation is a relatively crude measure of solar insolation. Potential annual solar insolation does not take into account topographic influences such as horizon shading nor does it weight radiation on east and west aspects differentially even though east-facing aspects have a higher daily heat load than western exposures (Dargie 1987). Solar insolation in this ecosystem is probably best measured in late winter and early spring when its effect on vegetation growth is greatest (Chiariello 1989) rather than the yearly average employed here. Furthermore, because blue oak grows more abundantly on north-facing aspects in the southern part of its range (Menke 1989), tree density likely reinforces solar insolation-related effects.

Slope is important in the three regions because it probably reflects the influence of livestock grazing on the vegetation since livestock grazing generally decreases with increasing slope (Mueggler 1965; Cook 1966; White 1966) and may accentuate vegetation patterns created by solar insolation, elevation and soil factors (Milchunas et al. 1989).

An unexpected result of this study is the emergence of A-horizon coarse fragment content as a factor affecting vegetation patterns in Avenales and Branch Mountain. A-horizon coarse fragment influences soil properties in very complex ways and we can only speculate on its potential significance. Coarse fragment may indirectly create a soil productivity gradient. According to this hypothesis, as coarse fragment content increases, soil productivity decreases because there is relatively less volume of soil and therefore relatively less mineral nutrients and organic matter available for plant growth. Hildebaugh (1984), however, found no consistent effect of A-horizon rock fragments on yields of crops, pasture or woodlands but, as he points out, there has been little research on the effects of rock fragments on soil productivity. A-horizon coarse fragment also may reflect a moisture gradient that available water capacity is not measuring. Again, the effects of coarse fragments on soil water are complex. For example, in some soils coarse fragments can increase rather than decrease water available to plants if the rock fragments are porous (Hanson and Blevins 1979). Vegetation gradients in this study, however, suggest that coarse fragments are decreasing soil water. Another unknown factor is the distribution of oak roots in the A-horizon and how they may be directly influencing the water available to the herbs especially when coarse fragment content is high.

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