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CONTROL OF VEGETATION ON CONTRASTING SUBSTRATES: HERB PATTERNS ON SERPENTINE AND SANDSTONE[1]

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ABSTRACT

Binary discriminant analysis (BDA) reveals relationships between species distributions and environmental variables. In this study, BDA was applied to transects on serpentine and sandstone in the Wenatchee Mountains, Washington. Species presence and states of ten habitat variables were recorded in each quadrat. Species response patterns significantly different from a random expectation suggested that distributions are controlled by soil moisture far more strongly on serpentine than they are on sandstone, where light and its correlates are more important. Environmental patterns were explored with direct principal components analysis (PCA) of standardized environmental variables and indirectly by PCA of the significant D-values. The latter is biased towards variables to which species respond strongly. The results emphasize the environmental and floristic contrasts between substrates. On serpentine, direct PCA indicates that effective moisture, soil fertility, and insolation control the first three axes, while on sandstone, insolation, fertility, and effective moisture control the first three axes, respectively. The PCA of D-values (Q-mode) is similarly interpreted: moisture is strongly correlated with the first component on the serpentine transect, while insolation and fertility are correlated with the first component on sandstone. Species ordinations also result from Q-mode analysis. They reflect species responses to the identified gradients and indicate mutual species-environment interactions. These analyses conform to the hypothesis that mineral conditions of serpentine select against intolerant species and that survivors respond primarily to moisture conditions that are a result of low productivity, attributable to adverse nutrient conditions. On sandstone, the moisture gradient is less pronounced, and direct canopy effects that create variable light conditions predominate. BDA is a useful tool in ecological survey and pattern analysis. Species responses to environmental factors may be estimated quickly and directly. This method will help to focus subsequent research, improve experimental design, and generate explicit and testable hypotheses about species-habitat interactions.

THE ABRUPT STRUCTURAL TRANSITION from normal to serpentine soils is one of the most dramatic vegetation patterns encountered in the Pacific Northwest. Species composition on serpentine soils is determined ultimately by the unique mineral composition derived from several forms of ultramafic parent rocks. Such soils are deficient in calcium, nitrogen, and other nutrients, while rich in magnesium and often one or more toxic heavy metals. Contacts between serpentine and more typical soils are marked by a dramatic alteration of species composition and productivity. While the fundamental causes of such changes have received much attention (e.g., Kruckeberg, 1969), less attention has been paid to how serpentine conditions alter other environmental parameters. In this paper, I compare the vegetation of a serpentine transect with one on sandstone and contrast the apparent differences in how environmental patterns are related to vegetation patterns.

Serpentine conditions appear to reduce productivity of dominant vegetation to produce a distinctly xeric complex of interacting habitat variables (cf., Whittaker, 1960). Particularly favorable environmental conditions appear to overcome the mineralogical effects (del Moral, 1974).

Species composition changes quickly along the serpentine transect. Such high beta diversity creates difficulties with the use of most analytical methods. During this investigation, I explored principal components analysis (PCA), multiple regression, multiple discriminant analysis (MDA), canonical correlation, and several classification methods. Each reveals aspects of underlying pattern, but confidence in the results is defeated by intractable problems such as nonlinear species response functions. Therefore I used a nonparametric

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TABLE 1. *Parent material, texture (2-mm fraction), calcium and magnesium (meq/100 g), Ca/Mg, and pH for soils representative of the transects studied. (Data from Kruckeberg, 1969, used by permission.)*

Parent material	Location	Ca	Mg	Ca/Mg	pH	Texture
Peridotite	Mesic flat	4.9	16.9	0.33	6.4	38
Peridotite	Dry flat	0.6	3.1	0.2	6.8	28
Peridotite	Dry flat	1.9	4.1	0.5	6.6	59
Peridotite	Barrens	0.3	3.7	0.12	7.6	38
Sandstone	Mesic flat	1.5	0.0		6.1	50
Sandstone	Dry flat	2.7	0.7	3.4	5.3	44
Sandstone	Dry flat	3.8	0.1	38.0	5.7	49
Sandstone	Xeric slope	4.7	0.2	23.0	6.4	23

method described by Strahler (1977, 1978), binary discriminant analysis (BDA), to explore species-environment relations. Binary discriminant analysis is used to explore species patterns relative to discrete environmental states. It is computationally direct and readily interpretable, though not entirely unambiguous.

METHODS AND MATERIALS—*Study site*—I conducted this study along the upper North Fork of the Teanaway River in the Wenatchee Mountains, Washington (Lat. 47°20′N, Long. 120°50′W). I have previously described the forest vegetation of this drainage (del Moral, 1972, 1974, 1975). Geologically complex, ultramafic parent materials are frequently juxtaposed to more typical substrates. The vegetation then contrasts sharply both in physiognomy and species composition. I placed one transect on an outcrop of Mt. Ingalls peridotite (Pratt, 1958), an ultramafic rock that weathers to a fine green shingle. This transect began on the moist, flat, cool flood plain of the Teanaway River at 1,300 m and terminated 560 m upslope at 1,360 m. The serpentine qualities are mitigated on the flood plain by a mixture of non-serpentine alluvium, substantial leaching, and by reduced drought stress. Here *Abies amabilis, A. lasiocarpa, Picea engelmannii,* and *Tsuga mertensiana* dominate. The transect crossed a gentle slope with scattered *Pinus contorta, Pseudotsuga menziesii,* and *Abies lasiocarpa,* moved through a steeper slope with old *Pinus ponderosa* and *Pseudotsuga menziesii* and young *Abies lasiocarpa, Pinus contorta,* and *P. albicaulis,* and terminated on a barren scree on which only scattered *Pinus ponderosa* and *Pseudotsuga* survive.

A second transect was located 1 km downstream on the Swauk sandstone (Pratt, 1958). This transect began at 1,250 m on the floodplain and extended for 600 m upslope to an elevation of 1,300 m. The lower transect crossed a moist, flat, cool forest dominated by *Abies amabilis, A. lasiocarpa,* and *Tsuga mertensiana.* It proceeded through a narrow, open, steep bank with little tree cover on to a bench with *Abies grandis* and *Pseudotsuga.* The transect terminated in an open forest with *A. grandis, Pseudotsuga,* and *Pinus ponderosa.* No sample was obtained within 20 m of a dirt road that crosses both transects. Otherwise, 1-m^2 plots were established at 10-m intervals, except that where the slope was steep, plots were placed closer together.

Climate—Precipitation and other climatic data are lacking for this area. The sites are climatically comparable with about 100 cm precipitation per year, of which less than 10% occurs during the summer months (del Moral, 1974).

Soils—Typical soil conditions for the transects are shown in Table 1, compiled from Kruckeberg (1969). Soils on peridotite are variable with respect to calcium and magnesium, but their ratio generally decreases with decreased drought. Sandstone soils have more calcium and less magnesium and their ratio is usually much higher. Soil pH is similar in mesic sites but otherwise more than 1 unit lower on sandstone than on peridotite. Soil pH indicates the severity of the serpentine effect (Kruckeberg, 1969).

Sampling—I recorded herb layer cover percentages within 1.0-m^2 quadrats. Habitat data were gathered at each plot and for some analyses they were converted to discrete, ordered classes. The ranges of each variable in each state on the two substrates are listed in Table 2.

Soils were collected to determine gravimetric soil moisture, organic fraction (loss on ignition at 500 C in 24 hr), texture (hydrometer method), and pH (1:1 paste equilibrated for 24 hr). Light was recorded relative to full sunlight between 11:00 and 13:15 PST. Soil tempera-

TABLE 2. *Environmental variables and states assigned to each on serpentine and sandstone substrates. The scale is the same for both substrates except in the case of slope*

Variable	Character state 1	2	3	4
Light—% full sun				
—serpentine	25	26–45	46–80	80
—sandstone	20	21–40	41–80	80
Canopy—% covered				
—serpentine	0	1–25	26–75	75
—sandstone	10	11–45	46–75	75
Exposure—to direct sun				
—serpentine	floodplain	moderate	exposed	
—sandstone	floodplain	protected	moderate	exposed
Slope—both soils	flat	gentle	moderate	steep
Soil temperature—°C				
—serpentine	11	11		
—sandstone	4	5–10	10	
Soil texture—% clay				
—serpentine	15	16–24	24	
—sandstone	15	16–19	19	
Soil organic—percentage				
—serpentine	10	11–20	20	
—sandstone	10	11–15	15	
Soil pH				
—serpentine	5.8	5.9–6.2	6.3–6.9	6.9
—sandstone	5.3	5.4–5.8	5.9–6.2	6.2
Litter depth—cm				
—serpentine	0.1	0.5–1.0	1.5–4.0	4.0
—sandstone	0.1	0.5–1.0	1.5–3.0	3.0
Soil moisture—percentage				
—serpentine	15	16–30	30	
—sandstone	15	16–25	25	

tures were recorded with a telethermometer at 15 cm depth. A second set of temperature determinations was made at the completion of the first and the results were averaged. Other factors (exposure, slope, canopy percentage, and litter depth) were determined directly. Data for light and soil temperature were collected on two successive, sunny days on the two transects. The use of variable classes minimizes the effect of sampling error and inherent within sample variability.

There were 61 plots on serpentine and 55 on sandstone. Binary discriminant analysis requires that at least 4 plots occur in each variable state. Therefore, for most variables, the number of states and their ranges differ slightly.

Analytical techniques—I clustered the herbaceous vegetation of each transect using mutual information to estimate similarity (program MINFO, Goldstein and Grigal, 1972). Because any clustering algorithm may make inappropriate decisions due to unique features of the data, I refined the initial classification by stepwise multiple discriminant analysis. (See del Moral, 1975, for the virtues of this procedure and del Moral, 1979, for some drawbacks.)

Principal components analysis was used to study the structure of the environmental data. PCA is relatively free from quirks when the data matrix is full and the data are standardized. The BMDP statistical package (Dixon and Brown, 1978) was used for this analysis.

Binary discriminant analysis was described by Strahler (1978). This method is appropriate to sites with high species turnover (beta diversity) where one seeks patterns of relationships between species distributions and the environment. First, a table of species occurrences in each state of each variable is constructed. Patterns that differ significantly from a random expectation, determined from a G-

TABLE 3. *Mean cover percentages for revised clusters recognized on the serpentine transect*

	Cluster						
Species	A	B	C	D	E	F	G
Clintonia uniflora	9.0	2.2	0.2				
Achlys triphylla	6.5	3.3					
Rubus lasiococcus	5.0	0.2	0.1				
Tiarella trifoliata	1.3	0.2					
Valeriana sitchensis	1.7		0.1				
Rubus parviflorus	1.7	14.0					
Viola glabella	1.3	2.2	0.1				
Angelica arguta		19.7			0.2		
Erythronium grandiflorum			0.4	0.2		0.1	
Senecio integerrimus			0.3			0.2	
Hieracium albiflorum			0.2		0.2		
Carex geyeri			1.4	0.4	0.3	0.5	
Agropyron spicatum			4.2	24.6	1.2	2.9	3.4
Achillea millefolium			2.6	0.2		0.2	2.8
Senecio pauperculus			0.8	0.2	0.3	0.3	
Arctostaphylos nevadensis			40.0			5.1	
Juniperus communis					57.5	11.6	
Aspidotis densa					1.0	0.8	1.8
Douglasia nivalis							0.8

statistic (Sokal and Rohlf, 1969) similar to a Chi-square, are retained. Occurrences are standardized by the method of Haberman (1973) to yield D-values, where one D-unit indicates a one standard deviation departure from expectation. D-values may be inspected to indicate the degree to which a species is associated or disassociated with a particular condition.

Second, D-values are combined into a single matrix of r species and c variable states. Q-mode analysis by PCA determines each species location (factor score) on each synthetic axis (component) and estimates the correlation between these components and the environmental variables (factor loadings). Thus an ordination of species in some complex factor space is recognized. R-mode analysis is a PCA performed on the transposed matrix. The initial solution is rotated so that a relationship between species (indicated by factor loadings) and principal components is revealed.

RESULTS—*Clustering*—The vegetation of each transect was clustered by MINFO and the results refined by SMDA. On serpentine, seven clusters were identified (Table 3). Only those 19 species with significant patterns determined by BDA are listed. Therefore, some dominant species restricted to a few quadrats are eliminated from the table. The groups are listed approximately along a moisture gradient, ranging from the floodplain communities (A, B) through a mixture of gentle, dry slope groups (C, D, E, F) to the steep scree group (G).

On sandstone, I identified eight groups, listed in Table 4. These groups are arranged approximately from open, moist sites through closed sites, to open, relatively dry sites. Species adapted to open conditions thus display a bimodal distribution (e.g., *Arenaria, Fragaria,* and *Viola*).

In each case, it is possible to distinguish among these species-defined groups on the basis of habitat conditions. On serpentine, discrimination between revised groups is best achieved using soil moisture, exposure, slope, soil temperature, and canopy cover, which are all direct moisture correlates. Light enters last in this analysis. On sandstone, soil temperature, organic fraction, slope, canopy cover, and light are the best discriminators. This analysis suggests that moisture is of prime importance on serpentine and that light is of prime importance on sandstone. However, the nature of the stepwise process and the fact that the discriminators are not independent does not engender great confidence in this result.

Principal components analysis—The standardized environmental variables of each transect were analyzed by PCA to reveal which factor varied most over each transect and to compare these results to both forms of discriminant analysis. The first three components account for 45.0%, 15.2%, and 9.5% of the variation. Factor loadings (eigenvectors) imply that Axis 1 is an effective moisture gradient.

TABLE 4. *Mean cover percentage of revised clusters recognized on the sandstone transect*

Species	Cluster							
	A	B	C	D	E	F	G	H
Cirsium edule	8.0	0.8	0.1					
Vicia americana	6.0	0.8	0.5					1.9
Arenaria lateriflora	2.0		0.3			0.1	0.8	0.5
Thalictrum occidentalis		9.8						
Hieracium albiflorum		0.6			0.2	0.3		0.2
Fragaria virginiana	5.7	16.8	1.7	0.2			0.8	7.2
Achlys triphylla	0.8	5.5					1.5	
Pyrola secunda		1.8	1.2	1.2	1.2			
Rubus lasiococcus		2.5	14.0	6.5	0.8	0.6	0.5	0.1
Spiraea betulifolia			2.0			0.2	0.3	
Viola glabella		2.3	3.1	0.2			0.2	1.2
Pachistima myrsinites			0.5	15.7	2.8	0.1	0.2	0.1
Vaccinium membranaceum				1.1	28.8	0.3	0.8	
Trillium ovatum		0.2	0.3	1.5	2.6	0.3	0.2	0.1
Lonicera ciliosa			0.3		1.2	0.2		
Clintonia uniflora				8.0	11.0	0.3	3.8	
Achillea millefolium	2.5	0.5		1.7	3.0			1.5
Rosa nutkana					1.2	4.0	3.0	0.5
Berberis nervosa				3.3	4.4	6.1	0.8	0.5
Symphoricarpos albus		1.0	2.4		1.2		10.5	
Angelica arguta			0.9					1.8
Rubus parviflorus			1.2	4.0	2.4	0.6	1.2	15.7
Pteridium aquilinum		0.8					7.0	20.2
Lupinus polyphyllus								10.0

The highest (absolute) factor loadings are soil temperature (0.43), soil moisture (−0.38), and litter depth (−0.40). Axis 2 suggests a fertility gradient because texture (0.72) and organic fraction (0.42) have the highest factor loadings though this axis may also relate to effective moisture. Axis 3 may be an insolation or light gradient since canopy percentage (0.62) and light (−0.51) are the main contributors.

The PCA of the sandstone transect shows less dominance by a single factor. The first three axes account for 31.9%, 22.1%, and 17.4% of the variance. Axis 1 is an insolation gradient dominated by light (−0.45), soil temperature (−0.48), and canopy percentage (0.44). Axis 2 appears to be a fertility gradient dominated by texture (−0.45) and organic fraction (0.42) and Axis 3 is a moisture gradient dominated by soil moisture (0.44) and texture (0.77).

Moisture effects dominate the serpentine transect and account for far more variance than they do on the sandstone transect, where no single factor dominates. It is of some interest that pH, which changes markedly along the serpentine transect, fails to appear as an important factor in this analysis.

Binary discriminant analysis, Haberman D-values—The analyses reported above made metric assumptions and do not clearly define relationships between species and environmental factors. They depend heavily on computational procedures that are cumbersome or impossible with large data sets and which usually distort the result.

Nineteen species occurred on serpentine with sufficient frequency to be analyzed by BDA, while there were 24 such species on sandstone. A sampling of results of phase I of BDA is shown in Fig. 1, which compares the preference patterns of species found on both substrates and gives representative patterns for other species.

Lines connect D-values for each state of a given variable to emphasize the response pattern. Positive scores imply preference, negative scores imply avoidance. In each case, 1 = low condition, 4 = high condition. *Achillea millefolium* (Fig. 1A, B) responds positively to increased light. It is more widely distributed on sandstone, and shows marked preferences for dry soil, warm temperatures, and reduced canopy only on serpentine. *Clintonia uniflora* (Fig. 1C, D) is a mesophytic herb. On serpentine it shows strong preferences for moist, cool, shaded, low pH sites. On sandstone, most sites are within the tolerances of this species so that it only shows a significant preference for temperature. *Rubus lasiococcus* (Fig. 1E, F) generally occurs in habitats somewhat drier than those of *Clintonia*. On serpen-

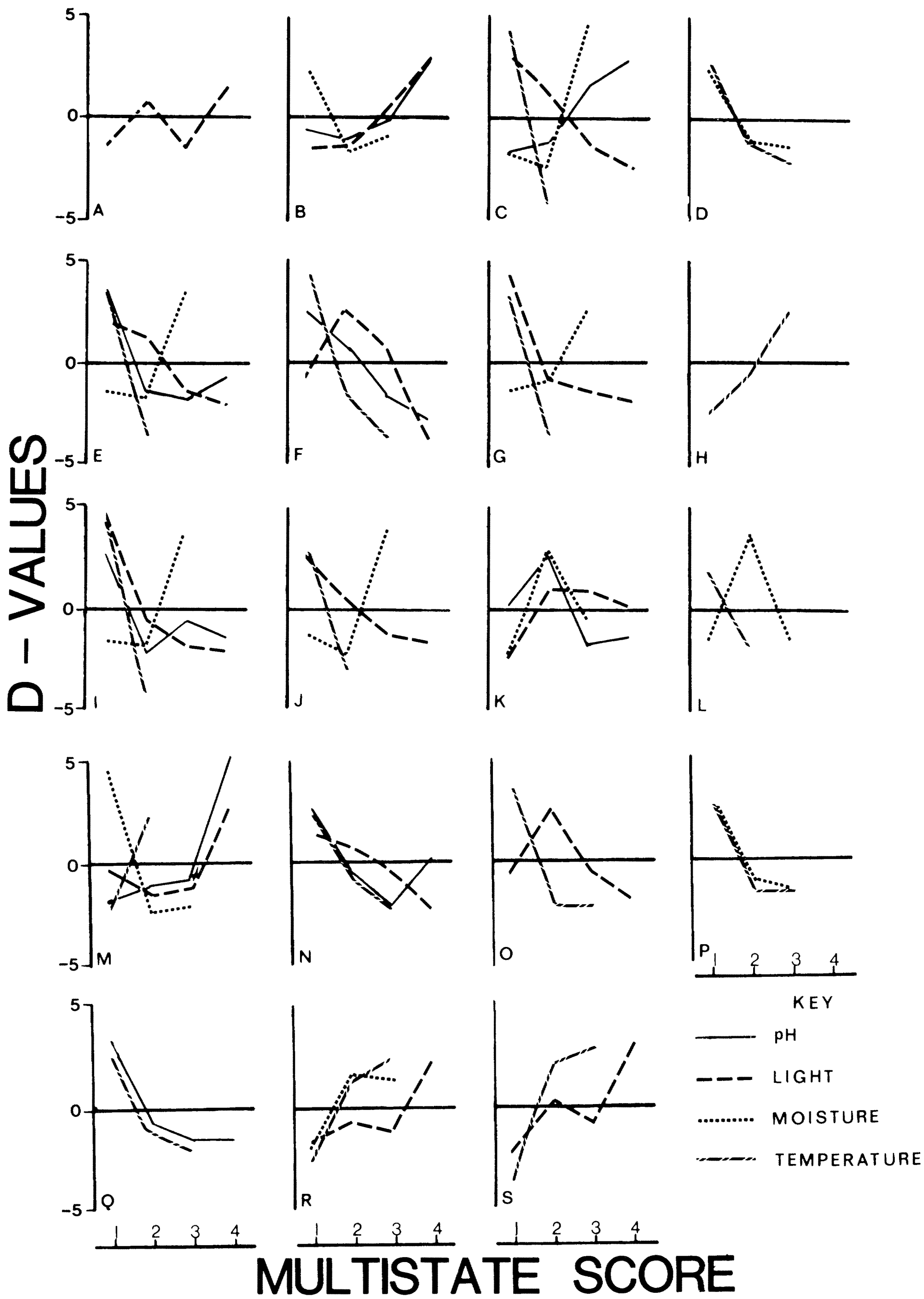

Fig. 1. Significant D-values for soil pH, light percentage, soil moisture, and soil temperature. In each case, 1 = low, 4 = high. Positive D-values indicate the species preference for the state, negative values indicate avoidance. Values at each state are connected to emphasize the response pattern. A = *Achillea millefolium,* serp.; B = *Achillea millefolium,* sand.; C = *Clintonia uniflora,* serp.; D = *Clintonia uniflora,* sand.; E = *Rubus lasiococcus,* serp.; F = *Rubus lasiococcus,* sand.; G = *Rubus parviflorus,* serp.; H = *Rubus parviflorus,* sand.; I = *Achlys triphylla,* serp.; J = *Viola glabella,* serp.; K = *Carex geyeri,* serp.; L = *Arctostaphylos nevadensis,* serp.; M = *Douglasia nivalis,* serp.; N = *Pyrola secunda,* sand.; O = *Trillium ovatum,* sand.; P = *Vaccinium membranaceum,* sand.; Q = *Pachistima myrsinites,* sand.; R = *Angelica arguta,* sand.; and S = *Pteridium aquilinum,* sand.

tine it prefers wetter sites, while on sandstone no such preference exists. Its response to the other factors is similar on both substrates. *Rubus parviflorus* (Fig. 1G, H) is a small shrub that prefers open, mesic conditions. On serpentine, it occurs only on the wetter, dark, cool sites, while on sandstone it only favors warmer sites. These comparisons suggest that species do not respond markedly to moisture levels on the sandstone transect. The entire transect is similar to moisture at the moist end of the serpentine transect. Sandstone conditions appear far less extreme than serpentine conditions with respect to moisture, pH, and related factors not shown.

Other species shown in Fig. 1 include a series of species from the serpentine transect arranged by moisture preferences (see Table 3). *Achlys triphylla* (Fig. 1I) strongly prefers mesic, shaded environments, while *Viola glabella* (Fig. 1J) prefers cool, moist habitats. *Carex geyeri* (Fig. 1K) prefers intermediate conditions with respect to moisture, light, and pH. The preferences of *Arctostaphylos nevadensis* (Fig. 1L), a prostrate woody species, are less marked because it is distributed patchily within an apparently homogeneous portion of the transect. It demonstrates preferences for warm sites of intermediate moisture conditions. (On nonserpentine parent materials in this region, such conditions would be considered xeric.) *Douglasia nivalis* (Fig. 1M) grows on the scree and demonstrates strong preferences for hot, dry, open conditions on virtually unweathered peridotite. Ten additional serpentine species were analyzed and showed a pattern with respect to at least one factor, but because of the small sample size, these preferences were not strong. No pattern contradicts evidence from field observation or other analyses performed in conjunction with this study.

The balance of Fig. 1 consists of six species from the sandstone transect. *Pyrola secunda* (Fig. 1N) is a common mesophyte found on acid soils. It shows a preference for low pH and a weak preference for cool, shaded sites. *Trillium ovatum* (Fig. 1O), a common lowland woods species, prefers the coolest, slightly more open sites. *Vaccinium membranaceum* (Fig. 1P), an understory dominant throughout much of this area which is confined to the wettest serpentine sites, is one of three species to show a significant moisture preference on sandstone. It is confined to the wetter, cooler sites. *Pachistima myrsinites* (Fig. 1Q), another common understory shrub, occurs on generally drier sites than *Vaccinium*. On this transect, it occurs in more acid, cool sites. *Angelica arguta* (Fig. 1R) is a mesophyte often

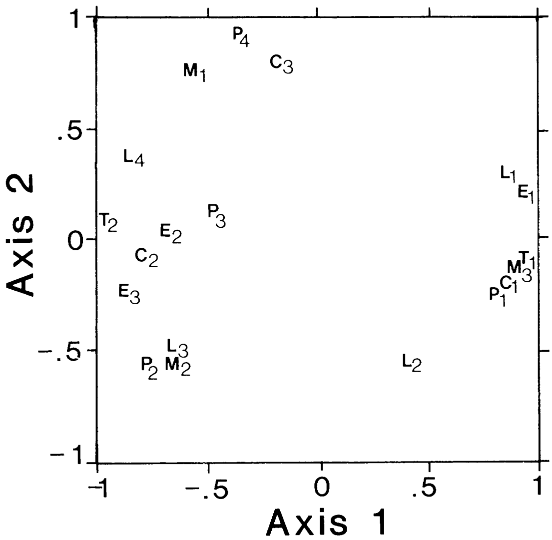

Fig. 2. Factor loadings of selected variables on serpentine, derived from Q-mode PCA. Each subscript indicates the variable state, from low to high. C = clay fraction; E = exposure; L = light; M = soil moisture; T = soil temperature; and P = soil pH.

found in open conditions. It demonstrates a preference for relatively warm, open, mesic sites and is confined to open quadrats near the river. Finally, *Pteridium aquilinum* (Fig. 1S) shows preference for warm, open conditions.

This discussion of the D-values suggests that the environmental control of the two transects differs markedly. Species respond differentially to a particular environmental variable on contrasting soils, either because the ranges differ (e.g., pH and soil moisture) or because interactions with other factors differ on the two substrates. Moisture scarcely appears as a controlling factor on sandstone, where light, canopy cover, and soil temperature are more frequently important.

Binary discriminant analysis—Q-mode analysis—The PCA of the matrix of D-values on each substrate reveals the contribution of each environmental factor to vegetation patterns. The results are consistent with those derived from the PCA of the standardized environmental factor scores described above. On serpentine (Fig. 2), the first three components account for 47.7%, 19.2%, and 12.0% of the variance. These axes can be interpreted by inspecting the distribution of factor loadings for each set of variables and by noting the mean position of species on the components. Axis 1 is a complex moisture gradient. Extreme states of exposure, soil moisture, temperature,

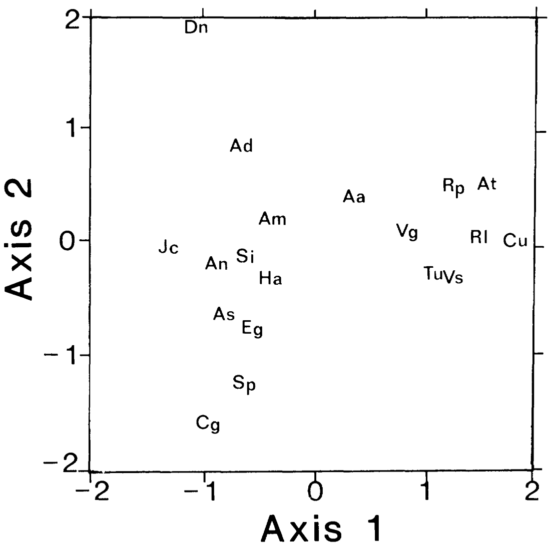

Fig. 3. Species distributions on serpentine, derived from Q-mode PCA. Species codes: Am = *Achillea millefolium*; At = *Achlys triphylla*; As = *Agropyron spicatum*; Aa = *Angelica arguta*; An = *Arctostaphylos nevadensis*; Ad = *Aspidotis densa*; Cg = *Carex geyeri*; Cu = *Clintonia uniflora*; Dn = *Douglasia nivalis*; Eg = *Erythronium grandiflorum*; Ha = *Hieracium albiflorum*; Jc = *Juniperus communis*; Rl = *Rubus lasiococcus*; Rp = *Rubus parviflorus*; Si = *Senecio integerrimus*; Sp = *Senecio pauperculus*; Tt = *Tiarella trifoliata*; Vs = *Valeriana sitchensis*; and Vg = *Viola glabella*.

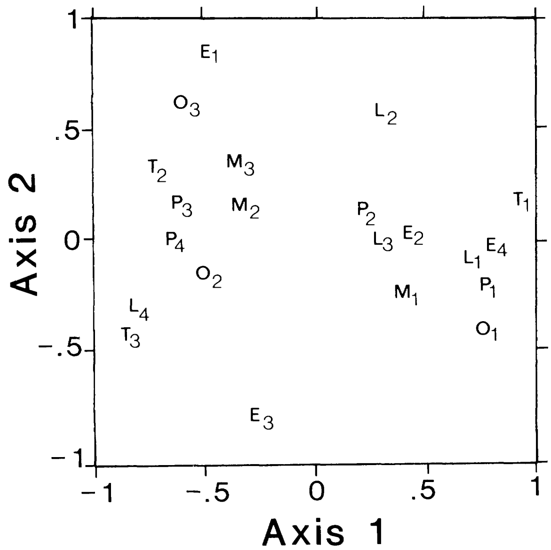

Fig. 4. Factor loadings of selected variables on sandstone, derived from Q-mode PCA. Each subscript indicates the variable state, from low to high. E = exposure; L = light; M = soil moisture; O = organic fraction; P = soil pH; and T = soil temperature.

and litter depth all have large eigenvectors. Axis 2 explains much less of the variation and is related to pH, soil texture, and slope. The implied gradient may be a measure of serpentine severity or an index of fertility. The most extreme of these serpentine soils are basic, have high clay content, and occur on the steepest slopes. The third axis is weakly and nonlinearly related to light.

Figure 3 shows species factor scores on the first two PCA axes for the serpentine transect. (These scores are the weighted mean position of a species with respect to the components identified above.) The interpretation of these axes is enhanced by consideration of the species distributions and knowledge of their general ecological requirements (cf., del Moral, 1974).

In Fig. 3, Axis 1 is a distinct moisture gradient from species centered in dry (negative) habitats to those centered in wet (positive) habitats. Axis 2 shows little variation in the moist end. However, a pronounced gradient, from *Carex geyeri* (Cg) to *Douglasia nivalis* (Dn), corresponds closely to the previously identified serpentine severity (or fertility) gradient. Species centered on the lower (negative) part of Axis 2 occur on the lower part of the transect above the floodplain. *Aspidotus densa* (Ad) and *Douglasia,* centered on the upper (positive) part of Axis 2, are found primarily on the scree slope.

The factor loadings for important variables on sandstone are plotted in Fig. 4. The first three axes contribute 32.2%, 15.8%, and 12.1% of the variance. Axis 1 is an insolation gradient, an assertion based on large factor loads for soil temperature, light, canopy cover. The second is less well defined, but exposure, slope, and texture have large factor loads, but moisture does not. This axis may reflect a fertility gradient or possibly an indirect moisture gradient based on evaporative demand. Axis 3 probably reflects soil moisture directly since this is the only variable with relatively large, consistent loadings and since moisture has low factor loadings on the first two axes.

The species scores are more gradational on sandstone than on the serpentine transect (Fig. 5). Species in the negative part of Axis 1 are better adapted to well lighted conditions, with preferences shifting towards deep shade in the positive half. Axis 2 is related to slope, from steep slopes in the negative portion to flats in the positive portion. Both soil fertility and soil moisture may be affected by this gradient. Since moisture does not affect this axis strongly, the fertility explanation may be more valid.

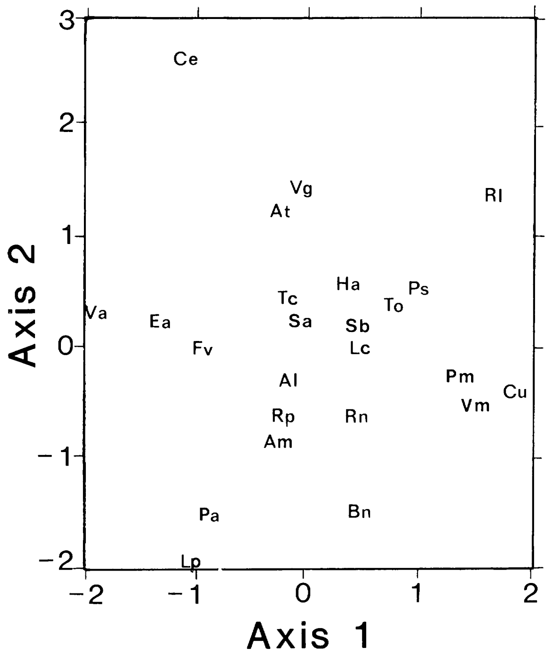

Fig. 5. Species distributions on sandstone, derived from Q-mode PCA. Species codes: Am = *Achillea millefolium*; At = *Achlys triphylla*; Al = *Arenaria laterifiora*; Bn = *Berberis nervosa*; Ce = *Cirsium edule*; Cu = *Clintonia uniflora*; Ea = *Epilobium angustifolium*; Fv = *Fragaria virginiana*; Ha = *Hieracium albiflorum*; Lc = *Lonicera ciliosa*; Lp = *Lupinus polyphyllus*; Pm = *Pachistima myrsinites*; Pa = *Pteridium aquilinum*; Ps = *Pyrola secunda*; Rn = *Rosa nutkana*; Rl = *Rubus lasiococcus*; Rp = *Rubus parviflorus*; Sb = *Spiraea betulifolia*; Sa = *Symphoricarpos albus*; Toc = *Thalictrum occidentalis*; To = *Trillium ovatum*; Vm = *Vaccinium membranaceum*; Va = *Vicia americana*; and Vg = *Viola glabella*.

Species distributions on the third axis do not yield to a simple interpretation, suggesting that the transect is not strongly differentiated with respect to moisture.

Binary discriminant analysis—R-mode analysis—The species factor loadings and the variance associated with each axis following R-mode PCA with varimax rotation are shown in Table 5 (serpentine transect) and Table 6 (sandstone transect). This analysis seeks species groups with similar responses to environmental factors. Rotation often sharpens the relationship between a principal component and the original environmental variable.

The first axis of the serpentine data accounts for only 30.5% of the variance but segregates the species into several groups. The first six species (Table 5) are those of moist, cool, dark forest sites. The next two (*Angelica* and *Viola*) occur together on the first axis; both occur on the floodplain but only *Angelica* occurs along the creek in more open sites. The next four species occur on the gentle, drier slopes. *Erythronium,* a spring ephemeral, and *Arctostaphylos,* a drought endurer, usually co-occur in intermediately moist sites. They are separated from *Hieracium* and *Senecio integerrimus* on the second axis in that they occupy shaded sites. Except for *Agropyron,* the remaining species found on the drier slopes display no second axis preferences. *Agropyron* appears to grow in plots receiving some conifer shading. In a data set with intrinsic discontinuity, the effect of R-analysis, compared to Q-analysis, is to combine information on the first axis and to make subsequent axes indistinct.

TABLE 5. *Factor loadings of species from serpentine transect on the first three components of R-mode analysis*

Species	Factor 1	Factor 2	Factor 3
Tiarella trifoliata	.961	−.420	.078
Rubus parviflorus	.930	−.031	.058
Rubus lasiococcus	.897	−.072	.311
Clintonia uniflora	.790	.462	.350
Achlys triphylla	.756	−.570	.078
Valeriana sitchensis	.404	−.108	.898
Angelica arguta	.098	.980	.120
Viola glabella	.054	.399	.904
Erythronium grandiflorum	.008	.988	.090
Arctostaphylos nevadensis	.004	.988	.087
Hieracium albiflorum	−.073	.001	.053
Senecio integerrimus	−.084	−.103	.974
Agropyron spicatum	−.223	.737	−.273
Achillea millefolium	−.296	−.011	.099
Senecio pauperculus	−.350	.009	.020
Douglasia nivalis	−.381	−.042	−.041
Aspidotis densa	−.384	−.006	.054
Carex geyeri	−.389	.035	−.036
Juniperus communis	−.742	.031	−.048
Percent variation	30.5%	22.6%	13.7%

Table 6 reveals a similar pattern on the sandstone transect. Variance partitioning is similar to that of Q-mode. Axis 1 is a pronounced gradient from species confined to deep shade (*Chimaphila, Pachistima*) to those with marked preferences for open sites (*Vicia, Epilobium*). The second axis is indistinct, with many species showing no preferences. A weak gradient from moist to dry conditions may be implied. Clusters are less distinct than on the serpentine transect, suggesting less coenocline differentiation.

DISCUSSION AND CONCLUSIONS—*Contrasts between the transects*—My earlier statistical

TABLE 6. *Factor loadings of species from the sandstone transect on the first three components of R-mode analysis*

Species	Factor 1	2	3
Vicia americana	.827	−.022	.396
Epilobium angustifolium	.740	−.015	.285
Cirsium edule	.666	−.121	−.210
Thalictrum occidentalis	.527	.299	−.266
Pteridium aquilinum	.523	−.029	.573
Achlys triphylla	.390	−.182	−.387
Lupinus polyphyllus	.342	−.196	.850
Rubus parviflorus	.335	.005	.583
Fragaria virginiana	.334	.824	.248
Viola glabella	.197	−.280	−.710
Achillea millefolium	.085	−.049	.739
Arenaria laterifolia	.084	−.042	.463
Symphoricarpos albus	.025	−.069	.082
Spiraea betulifolia	.009	.927	.013
Hieracium albiflorum	.016	.012	−.273
Rubus lasiococcus	−.084	−.977	−.099
Rosa woodsii	−.084	−.046	−.041
Pyrola secunda	−.275	.924	−.150
Berberis nervosa	−.389	−.011	.120
Trillium ovatum	−.618	−.006	−.381
Lonicera ciliata	−.639	.018	−.188
Vaccinium membranaceum	−.802	.029	.059
Pachistima myrsinites	−.826	.041	−.120
Chimaphylla umbellata	−.887	.055	−.092
Percent variation	28.5%	15.4%	14.8%

studies of these transects revealed general patterns but contained sufficient ambiguities and contradictions to render the results unsatisfactory. That the data fail to even approximate the statistical assumptions of these methods caused further concern. A nonmetric approach was indicated. Though not without drawbacks, BDA appears to mitigate some inherent difficulties with analyses of species patterns along environmental gradients.

Principal components analysis was applied to the standardized environmental data to serve as a basis for comparison. This method seeks an overall pattern of environmental variation, but does not consider species responses to a unit of environmental change. Species may respond greatly to changes in one variable and little to changes in another, but such differences do not necessarily manifest themselves in PCA.

On serpentine, Axis 1 is dominated by moisture-correlated factors, Axis 2, by fertility-related factors, and Axis 3 appears to be an insolation gradient. On sandstone, Axis 1 is dominated by insolation-correlated factors, Axis 2 by fertility-related factors, and Axis 3 by moisture-related factors. These results are interpreted to mean that habitat structure on each substrate is distinctive.

Multiple discriminant analysis of groups based on species composition using habitat factors as discriminators, does not readily reveal the control of vegetation by environment. It is constrained by linear assumptions, confounded by factor interactions, and apparently sensitive to sampling error. The results are also sensitive to the precise configuration of the groups and minor revisions often result in different rank order of discriminant variables. While the results from multiple discriminant analysis partially confirm the interpretations from other methods, they do not stand alone.

Binary discriminant analysis is an essentially nonmetric method. The importance of each variable to individual species is determined directly and the assumption that distributional correlation implies causal effects can, once identified, be tested. D-values indicate that on serpentine, 12 of 19 species respond to soil moisture while on sandstone only 3 of 24 do so. In contrast, equal proportions of species respond to light (12 of 24 on sandstone and 9 of 19 on serpentine) and soil temperature is more important on sandstone (16 of 24 species) than on serpentine (10 of 19 species). Such results reinforce the observation that moisture is more important on serpentine than sandstone, and they generate distinct, specific, and testable hypotheses about individual species.

Q-mode analysis by PCA provides estimates of the importance of environmental factors to the control of the vegetation. However, rather than standardized habitat values, the relationship between D-values is explored. Significant D-values express the strength of a relationship between species and environment, and therefore this analysis is biased in favor of those variables actually correlated with species patterns. There is a countervailing tendency: the second axis is often distorted because intermediate values of variables given high weight on Axis 1 may be placed on extremes of Axis 2. However, this effect is not extreme when the environmental variables are not strongly correlated.

The results of Q-mode analysis of D-values do not materially contradict those of direct PCA. On serpentine moisture, serpentine severity, and light appear to be the major factor complexes. Because variation is concentrated on the first two axes, the third axis is less readily interpretable. On sandstone, light or insolation, fertility, and moisture gradients are identified. These contrasts between substrates agree fully with results of other approaches.

Q-mode analysis of species distributions results in distinct ordinations. Species relationships are clear and predictions about relative drought tolerances, for example, readily emerge. Whereas D-values indicate how a species relates to a single measured factor, Q-mode analysis suggests how a species relates to a factor complex and how the species interrelate.

R-mode analysis of species distributions (factor loadings) is similar to that of Q-mode analysis in each transect. Where several variables are combined, as in this study, the tendency of species to form clusters, noted by Strahler (1978), is reduced. Rotation of the axes appears to concentrate the bulk of the interpretable information on the first axis.

The methods converge to a single conclusion. The overriding environmental variable on the serpentine transect is effective moisture. On the floodplain, the alluvium is a varied mixture of materials. Under these mesic and relatively fertile conditions, continuous conifer cover is possible, thus creating deep shade, increased acidity, a cool and moderate temperature regime, and favorable conditions for herb growth. Tree species composition shifts from *Abies amabilis, A. lasiocarpa* and *Picea engelmannii* on the floodplain to *Pseudotsuga* and *Pinus contorta* on gentle serpentine slopes where the soil is less weathered and retains a moderate magnesium to calcium ratio that reduces productivity and enhances evapotranspiration. On steeper slopes, runoff is rapid, weathering slow, and serpentine conditions extreme. Here, only a few *Pinus ponderosa* and *Pseudotsuga* individuals survive. Productivity and cover are low and drought is pronounced. Thus, while edaphic factors on serpentine alter species composition and may lead to the formation of ecotypes (Kruckeberg, 1969), the immediate ecological manifestation is that of a steep moisture gradient.

In contrast, soil moisture conditions on the sandstone transect are never extreme. The analysis suggests that insolation (e.g., temperature and light) creates the greatest species differentiation. Moisture contrasts exist, particularly between the lower floodplain and plots in canopy gaps, but in contrast to the serpentine transect, understory vegetation is at a minimum where conifers exert their greatest dominance, and temperatures and light levels are lowest.

Under serpentine conditions, productivity and cover are so reduced that moisture controls species distributions. Where moisture conditions are especially favorable, the understory vegetation is scarcely distinguished from that found in mesic forest understories on sandstone.

Evaluation of BDA—Binary discriminant analysis could play a useful role in ecological survey work, experimental design, hypothesis generation, and remote sensing studies. It is rapid and inexpensive with substantial heuristic value, quickly sorting out relationships between environmental patterns and species distributions. At early stages of an investigation, BDA offers advantages unmatched by other methods. It mitigates statistical problems associated with standard multivariate methods. A less appreciated virtue is that environmental pattern is analyzed (Q-mode) after species response functions are determined. This effectively weights variables that appear correlated to species patterns.

Binary discriminant analysis is not free from defects. The relative importance of environmental variables cannot be determined directly and difficulties due to factor interactions are not resolved. As with other techniques, only statistical associations are revealed. The method contributes nothing to a true understanding of ecological causality. Where environmental responses are combined, R-mode appears to provide few additional insights.

Two further steps are suggested by these defects. After correlations are revealed, derivative hypotheses may be tested experimentally. For example, I suggested that it is moisture, not adverse mineral effects, that restricts species on serpentine. It follows that floodplain species should grow on the gentle serpentine slopes if sufficient water were provided, taking care not to leach the soil.

A complementary approach is to develop behavior models for each species in response to a factor complex using path analysis or other forms of regression. Such a method would reveal the interaction among habitat variables.

Binary discriminant analysis overcomes numerous problems familiar to field ecologists and promises to become an integral tool in ecology. It will enhance the efficiency of ecological survey work, improve gradient analysis investigations, promote more efficient experimental design, and make more explicit the relationships between plants and their environment.

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