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Among-site Variation in Riparian Vegetation of the Southern California Transverse Ranges

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ABSTRACT.—Data from 37 sites in the Transverse Ranges in southern California were used to assess the influence of a variety of environmental variables on among-site variation in riparian vegetation. Ordination and regression analyses indicated that elevation, unit stream power, fire history and valley width all have significant impacts on the composition of this vegetation. TWINSPLAN classification generated four species groups: a *Baccharis glutinosa*/*Salix laevigata* group that appears related to low elevations, high stream power and recent fire; a *Populus fremontii*/*Alnus rhombifolia* group associated with high stream power, but longer time since burning and higher elevations; a *Salix lasiolepis*/*Rosa californica* group typically found at high elevation sites with low stream power; and a *Platanus racemosa*/*Adenostoma fasciculatum* group that did not show a clear environmental preference.

INTRODUCTION

Attempts to explain the distribution and composition of riparian vegetation have frequently emphasized within-site rather than among-site environmental variables (Baker, 1989a). Researchers typically have devoted themselves to explaining the bands of vegetation that often parallel stream channels and form a compositional gradient across the valley bottom. The resulting studies therefore have emphasized environmental factors that vary across a given valley bottom locale: flood frequency (Illichevsky, 1933; Sigafoos, 1961; Bendinger, 1971; Bell, 1974, 1980); depth to water table (Frye and Quinn, 1979); landform position (Hupp and Osterkamp, 1985; Harris, 1987); successional status (Fonda, 1974; Smith, 1980; McBride and Strahan, 1984a); substrate particle size (Osterkamp and Hupp, 1984; McBride and Strahan, 1984b) and stream power (Bendix, 1992).

Within a given region, however, riparian vegetation may also show considerable among-site variation, *i.e.*, overall composition varies among different valley-bottom sites (Roberts, 1984; Brothers, 1985; Harris, 1988; Baker, 1989b). Such variation suggests a possible influence by among-site variables; that is, environmental factors that vary among valley-bottom sites, rather than across a given valley bottom (Hupp, 1982; Baker, 1989a). This study focusses on the environmental relationships that may be active at the among-site scale, with the complete valley bottom cross-section as the unit of analysis. It uses ordination, regression and classification techniques to examine several among-site environmental variables, and test their influence on the among-site variation in woody species composition within two watersheds in the Transverse Ranges of southern California.

Previous studies of among-site relationships in California riparian vegetation have been largely descriptive (*e.g.*, Roberts, 1984; Brothers, 1985). Indeed, there is a dearth of quantitative studies on this topic in the western United States, with the notable exception of Baker (1989a, 1990). The existing literature did, however, suggest a number of among-site variables whose influence could be tested in this study.

Brothers (1985) noted differences in vegetation related to valley aspect and watershed size. Even within a single small watershed, vegetation has been found to change with elevation (Parikh and Davis, 1986). Parikh (1989) also found some species were limited to sites with permanent surface or near surface water, which she related in turn to local bed-

rock lithology. Fire history is another among-sites variable with potential influence on riparian vegetation. While they do not address the issue in terms of spatially varied impacts, Parikh (1989), Barro *et al.* (1989) and Davis *et al.* (1989) all discuss impacts of fire on southern Californian riparian species. A number of studies from ecological and management perspectives have pointed out the impacts of livestock grazing on riparian vegetation (*e.g.*, Martin, 1979; Shanfield, 1984; Smith, 1989). These impacts may also vary between sites that have experienced different intensities or histories of grazing pressure.

Baker (1989a, 1990) identified a suite of additional among-site variables, including valley dimensions, relief ratio, drainage density, ruggedness, and drainage basin length, orientation, relief and elongation. Many of these variables (along with drainage basin size, which was mentioned earlier) owe their potential for influencing vegetation to their influence on flood characteristics (Patton and Baker, 1976; Baker, 1989a). Flooding, in turn, may influence the vegetation through differential species susceptibility to its mechanical impacts, through the removal of vegetation and initiation of successional processes or through reworking of alluvial substrate (Bendix, 1992).

The impact of flooding may be mediated by details such as seasonality, duration, and the sediment available to be transported, but one of the most important characteristics of a flood is the energy it applies to mechanical work, including destruction of vegetation and sediment transport. This energy varies between sites in response to varying hydrologic and morphologic conditions. In the present study, site data were sufficiently detailed to estimate values for a measure of flood energy, unit stream power, at the study sites (Bendix, 1992). Because these stream power estimates encompass much of the impact of watershed hydrology, they replaced variables that had served as surrogates for hydrology in past research.

The inclusion of this range of environmental variables, some with detailed data that have not been available in previous studies (stream power, fire history for multiple burns), allows recognition of patterns of vegetation response to among-site environmental variation. It also allows autecological interpretation of the manner in which both individual species and groups of species are reacting within the overall pattern of vegetation response.

METHODS

Data collection.—Data were collected at 37 sites in the Piru and Sespe watersheds (Fig. 1). All sites were within the Los Padres National Forest, and upstream from any stream regulation. They were located so as to sample at regular intervals and represent the morphologic variation of the valleys, while avoiding substantial impact by humans (jeep trails, highway embankments, etc.).

Data for each site included woody vegetation cover by species, and values for a suite of potentially important environmental variables (Table 1). Vegetation cover was measured by line intercept sampling (Canfield, 1941) along a single transect across the valley bottom, extending from one edge to the other of the flood zone for the 20-yr recurrence interval discharge (as delineated with the HEC-2 program, described below). Herbaceous vegetation was excluded to reduce the impact of seasonal variation during 4 mo of fieldwork. Cover for each species was summed for each site, and because site widths varied, the summed values were relativized for analytical purposes. Nomenclature for all species follows Munz and Keck (1968).

Unit stream power, the measure used for flood severity, is the power exerted by a flood per unit area of the wetted perimeter (Baker and Costa, 1987). It is calculated as

$$\omega = \gamma D S v \quad (1)$$

where ω = unit stream power in W/m^2 , γ = specific weight of the fluid in N/m^3 , D =

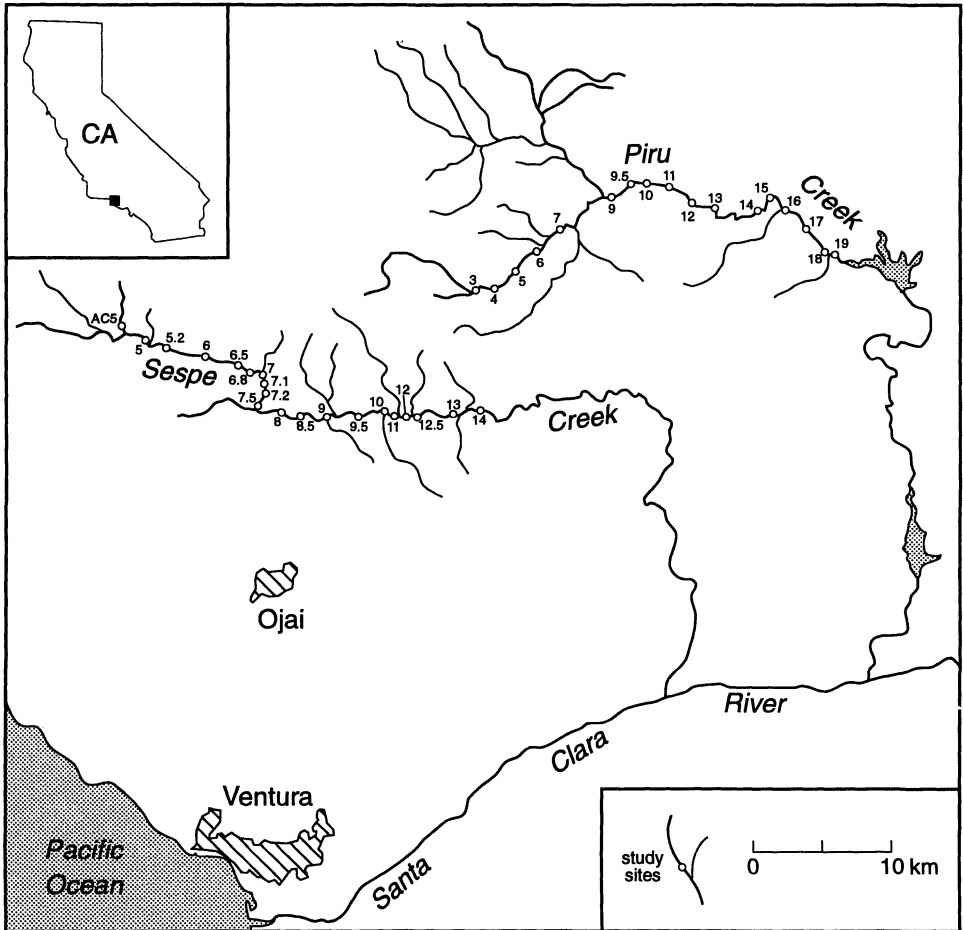


FIG. 1.—Location of study sites

depth of flow in meters, S = the dimensionless energy grade line, and v = flow velocity in m/s. In this analysis, γ was assigned a constant value of 9800 N/m^3 , following Costa (1983) and Baker and Costa (1987). D , S and v (along with the dimensions of the flood zone defining site limits) were all obtained as output from the hydrologic modeling program HEC-2 (Feldman, 1981; Hydrologic Engineering Center, 1991). The inputs for HEC-2 are the valley bottom dimensions, Manning's roughness coefficient (n), a slope estimate for the initial iteration, and discharge. Valley bottom dimensions were surveyed with level and rod along the vegetation sampling transect at each site; the variation of n across each site was calculated with an equation that sums values for discrete roughness elements (Arcement and Schneider, 1989); slope was estimated from topographic maps; and discharge for the 20-yr flood was estimated with an empirically derived regional flood frequency curve developed by the U.S. Army Corps of Engineers (1985), based on size, precipitation intensity and other characteristics of the drainage basin. The 20-yr recurrence interval was chosen because its lateral extent provides a reasonable and objective delineation of the riparian

TABLE 1.—Candidate environmental variables included in analyses

Variable	Units
Elevation	meters
Aspect	scalar
Grazing	dichotomous (0,1)
Fire history	years since last burned
Mean 20-yr stream power	W/m ²
Standard deviation of 20-yr stream power	W/m ²
Valley bottom width	meters
Lithology	generalized rock type

zone. Because of the steep relief, shallow soils and large winter storms that characterize the study area, the 20-yr discharge constitutes a major flood, which inundates the width of the valley bottom at most sites. Further details of these hydrologic calculations are presented elsewhere (Bendix, 1992).

Both the mean and the variance of unit stream power at each site were of interest. The mean provides a measure of the general severity of flooding at the site, which obviously has the potential to affect vegetation. It is also possible that the composition of vegetation at a site may reflect the distribution of power there, as a site that was subjected in its entirety to destructive impacts might support different vegetation than a site where these impacts ranged from minor to extreme. For this reason, rather than calculating total stream power across the site (Bagnold, 1966), each site was divided into 4-m segments, with unit stream power calculated for each. The mean and standard deviation of unit stream power were then calculated for each site.

Site elevation and valley bottom width were measured from USGS topographic maps (1:24,000). Valley bottom width might be considered an example of a variable acting indirectly, through its influence on the hydrologic characteristics already represented by the stream power variables. It was included, however, because it may have other environmental influences as well. Narrow gorge sites are often more shaded than wider valley bottoms, and generally appear to be more mesic. The down-valley azimuth at each site also was recorded from topographic maps, and was converted to a scalar of values representing potential heat load/solar exposure (Parker, 1980, 1982).

The measure used to assess the possible impact of fire was the number of years since each site had last burned. Forest Service records were examined to determine the most recent date when each site had been within fire boundaries. The 22% of the sites that had not burned within the period of record were assigned a time since burning equal to the length of the record (80 yr), since that constituted a minimum value for the variable. These records include all fires 10 acres or greater in area, and it is unlikely that smaller fires would have been so exactly placed as to have substantially affected the study sites. Some confirmation of this may be derived from the absence of charred logs and stumps at the sites shown as unburned in the records, which contrasted with the visible remnants at sites burned more recently.

Severity of livestock grazing could not be precisely measured because Forest Service grazing records are organized by broad areal grazing allotments, and do not indicate stocking levels along the creeks. Grazing therefore was recorded as a dichotomous variable, assigned a "1" if there was visible evidence of cattle, and a "0" if there was not. All of the sites with cattle sign were within the Piru Allotment, which includes some but not all of the sampling

sites on Piru Creek. This is, in fact, the only part of the study area that has been grazed in recent years, according to Forest Service records.

Lithology of each site was identified on 1:24,000 geologic maps (Dibblee, 1979a, *et seq.*), and confirmed by field observation of outcrops at several of the sites. Sites mapped as Quaternary alluvium were assigned the lithology of the adjacent mapped unit, on the assumption that this underlies the alluvium. Each site was classed as having one of five general rock types: crystalline, conglomerate, sandstone, shale and unconsolidated material.

Analysis.—Detrended correspondence analysis (DCA) (Hill and Gauch, 1980) was used to produce ordinations for both sites and species, with the CANOCO (v. 3.12) computer program (Ter Braak, 1985). Default options were followed in the ordination, which included 37 sites and 28 species. DCA was used because it circumvents the “arch-effect” common with other ordination techniques, in which the second axis often represents a quadratic distortion of the first (Gauch, 1982). Multiple regression provided a means of assessing the impacts of the environmental variables on the vegetation, as represented by the DCA scores. All possible combinations of the environmental variables were tested for inclusion in regression models predicting the site scores on the first and second DCA axes. Choice of the optimal model was based on the following criteria: improvement in adjusted R^2 ; overall model and parameter estimates significant at the 0.05 level; and parsimony. No models included any pair of variables with a Pearson’s correlation coefficient ≥ 0.80 , in order to avoid excessive multicollinearity.

Residuals from the final models were plotted against the explanatory variables and visually examined for signs of heteroscedasticity or autocorrelation. A check of outliers suggested no grounds for their removal, so all observations were used in the regression models (Draپر and Smith, 1981). Models are reported here with standardized coefficients, to aid in the comparison of the role of different independent variables. Bivariate plots and Pearson’s correlation coefficients between the chosen explanatory variables and the axis scores provided indicators of whether the predictors were influencing composition in a simple, direct manner, or through complex, complementary relationships.

Rather than including lithology among the candidate variables for the regression models (which would have required the unwieldy inclusion of four dummy variables), lithologic influence was tested by analysis of variance (ANOVA) of the residuals from the regression models. This approach tests whether the variable accounts for any of the variation left unexplained by the regression model.

While ordination, regression and ANOVA provided the means for testing environmental factors, classification provided an aid in interpreting results. Two-way indicator species analysis (TWINSpan), a polythetic, divisive technique, was used to produce interpretively meaningful groups of sites on the basis of compositional similarity and of species on the basis of distributional similarity (Hill, 1979). Breaks in the second and third levels of the classification were subjectively chosen to produce site and species groups that could be considered together in evaluating environmental relationships. This is an approach commonly adopted in vegetation analyses (Golden, 1979; Westman, 1983), although some recent studies have cautioned that DCA and TWINSpan may be unreliable under certain circumstances (van Groenewoud, 1992; Belbin and McDonald, 1993).

RESULTS

Ordination and regression.—The first and second DCA axes accounted for 43.3% and 27.9%, respectively, of the cumulative compositional variance encompassed in the first four DCA axes. This represents 24% of the overall variance in the data set. Site scores on the two axes were uncorrelated, with a Pearson’s correlation coefficient of 0.07 ($P > 0.05$).

TABLE 2.—Pearson's correlation coefficients between DCA site axis scores and environmental variables included in regression models predicting those scores

Variable	Axis 1	Axis 2
Elevation	0.68**	-0.14
Fire	-0.36*	-0.47**
Mean 20-yr stream power	-0.37*	-0.00
Valley bottom width	0.33*	0.20

* P < 0.05

** P < 0.005

Regression modeling of site scores showed the first axis is related both to elevation and to the mean value for unit stream power:

$$\text{AXIS1} = 0.644(\text{ELEVATION}) - 0.300(\text{MEAN STRMPWR}) \quad (2)$$

This model accounts for 55% of the variance in Axis 1 site scores, and is significant at the 0.001 level. Each of these explanatory variables is significantly correlated with AXIS 1 (Table 2), suggesting that positioning on this axis is in direct response to these factors. The pairing of the positive coefficient for elevation and a negative coefficient for stream power probably reflects the fact that high elevation sites tend to experience low stream power, because they are higher in the watershed, with smaller drainage areas and smaller discharges.

The best model for the second axis suggests that it reflects a more complex gradient, combining fire history, valley bottom width and, again, the mean value for unit stream power in the 20-yr recurrence interval flood:

$$\text{AXIS2} = -0.594(\text{FIREYRS}) + 0.409(\text{MEAN STRMPWR}) + 0.372(\text{WIDTH}) \quad (3)$$

Explained variance for this model is 36%, and the overall model is again highly significant ($P < 0.005$).

The bivariate correlation matrix (Table 2) shows that while fire history is strongly and significantly correlated with the second axis, stream power and valley width are not. The significant contribution of the latter variables indicates that they are contributing in a complex, complementary manner, perhaps reflecting the influence of valley morphology on the distribution of flood impacts. Thus, while AXIS 2 is considered for this discussion to reflect fire history, location on the axis should not be interpreted as a direct indicator of stream power or valley width.

The site ordination diagram does not show sites clustering according to lithology on either axis (Fig. 2), and ANOVA results bear out this impression. Lithology was not significant (at the 0.05 level) in explaining the residual variation in DCA axis scores from either of the regression models.

Environmental characteristics of sites.—TWINSPAN classification yielded four groups that show modest clustering on the DCA site ordination diagram (Fig. 3). Mean values and standard deviations for each group of the predictor variables from equations 2 and 3 are shown in Table 3. Although the variance for some groups is large, these values do provide indicators of the environmental characteristics of the habitat types represented by the TWINSPAN groups. The high values of mean unit stream power for some groups are comparable with the high range of published values in other settings (Baker and Costa, 1987); this reflects bedrock control at many sites that imposed unusually steep energy gradients (S in equation 1).

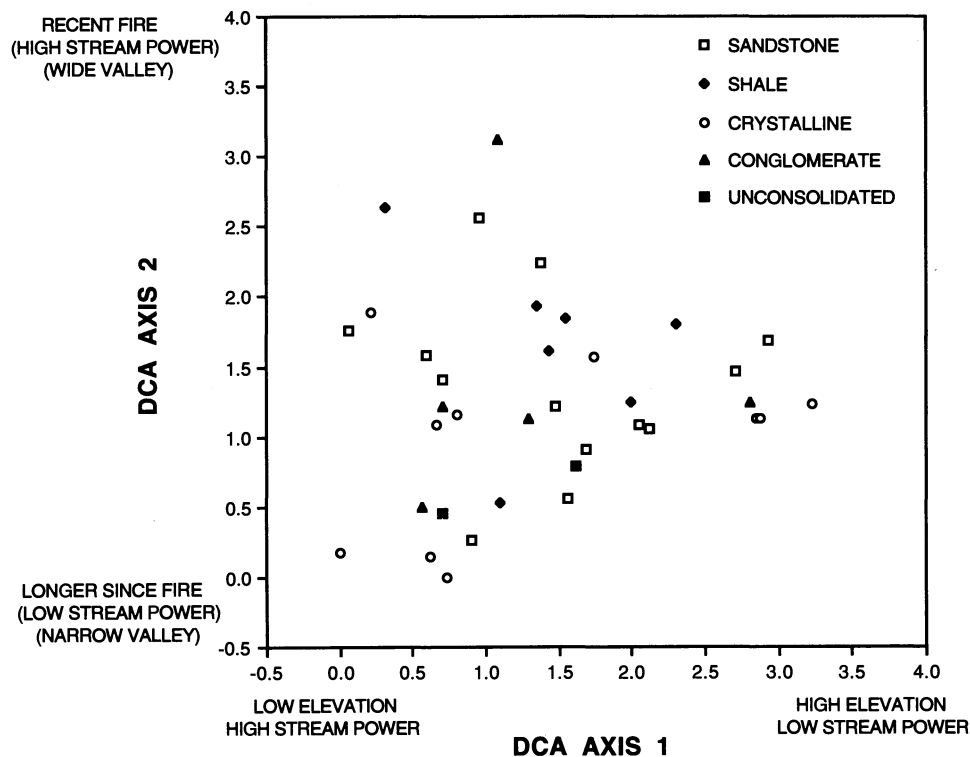


FIG. 2.—DCA ordination diagram of sites, by site lithology. Explanatory variables from equations 2 and 3 that are not directly correlated with axis scores are in parentheses

Groups 1 and 4 are characterized by relatively recent fire, but are distinguished by very different elevation and stream power values. Group 1 has much lower average elevation and much higher average stream power than group 4. While the position of specific sites on the ordination axes should be interpreted cautiously, these numbers are in accord with the relative positions of these groups in the site ordination diagram. They are the two higher groups on Axis 2, reflecting recent fire, and they are separated effectively on Axis 1, which was related to elevation and stream power.

Groups 2 and 3 have a longer average time since burning, but are also differentiated by elevation, with group 3 lower than group 2. Table 3 also suggests that the groups might be segregated by valley width; the failure of the ordination diagram to show this is in keeping with the lack of a direct correlation between valley width and Axis 2 (Table 2). In general, the relatively weak separation of the TWINSpan groups on the second axis reflects the weaker influence of the environmental variables it was regressed on, as indicated by comparison of explained variance from the models for the two axes.

Patterns of species response.—The TWINSpan classification also generated four groups of species that are somewhat clustered on a DCA species ordination diagram (Table 4, Fig. 4). Each group is identified by the two species within it with the greatest relative cover: *Baccharis glutinosa* and *Salix laevigata*; *Populus fremontii* and *Alnus rhombifolia*; *Platanus racemosa* and *Adenostoma fasciculatum*; and *Salix lasiolepis* and *Rosa californica*.

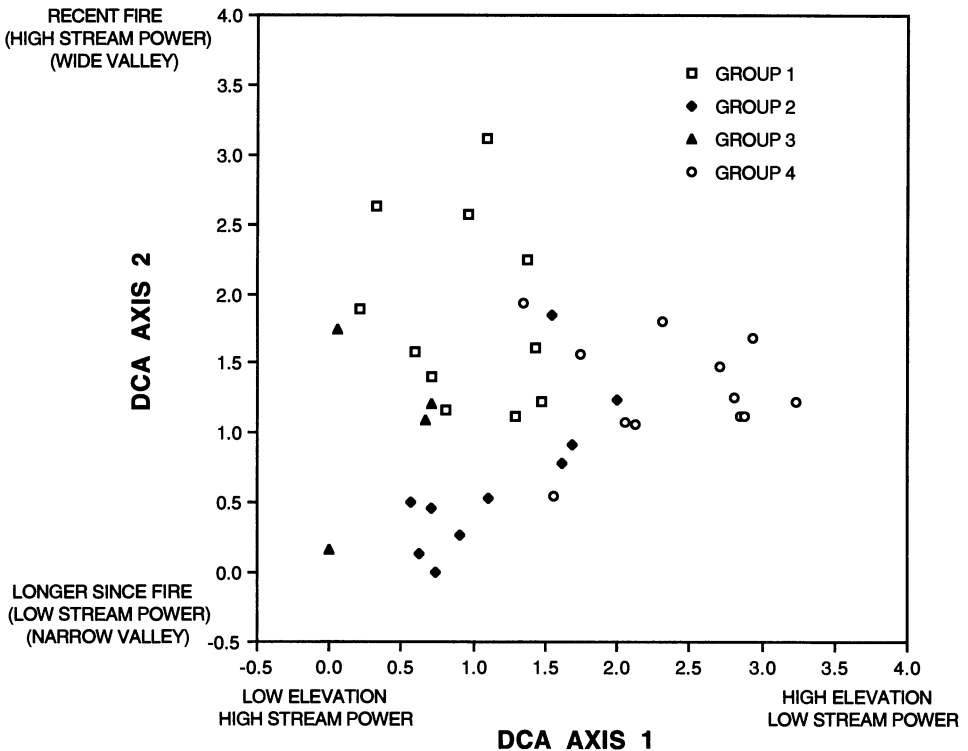


FIG. 3.—DCA ordination diagram of sites, by TWINSpan group. Explanatory variables from equations 2 and 3 that are not directly correlated with axis scores are in parentheses

Not surprisingly, these groups are somewhat coincident in their occurrence with groups from the TWINSpan site classification (Table 5). *Baccharis glutinosa* and *Salix laevigata* have the greatest cover within group 1; *Populus fremontii* and *Alnus rhombifolia* provide the most cover within group 2; and *Salix lasiolepis* and *Rosa californica* dominate the cover in group 4. The other species in the data set are similar, in that most reflect the general fidelity between site groups and species groups. The exception is the *Platanus/Adenostoma* species group, which has constituent species associated with each of the site groups.

DISCUSSION

Neither ordination scores nor average environmental conditions of classified site groups are sufficient to support definitive conclusions about individual species. This evidence does, however, indicate which environmental factors may be influencing species, thereby contributing to the overall compositional relationships shown by the DCA axis regression models. Bivariate Pearson's correlations between the more common species' relative cover and environmental variables add confidence to some of these speculations, and where such correlations are significant ($P < 0.05$), they are mentioned in the following discussion.

Site group 1, which was associated with the *Baccharis/S. laevigata* group, was characterized by low elevation, high stream power and recent fire (Table 3). The latter two variables suggest disturbance is an important factor for this habitat. This affinity for disturbed sites

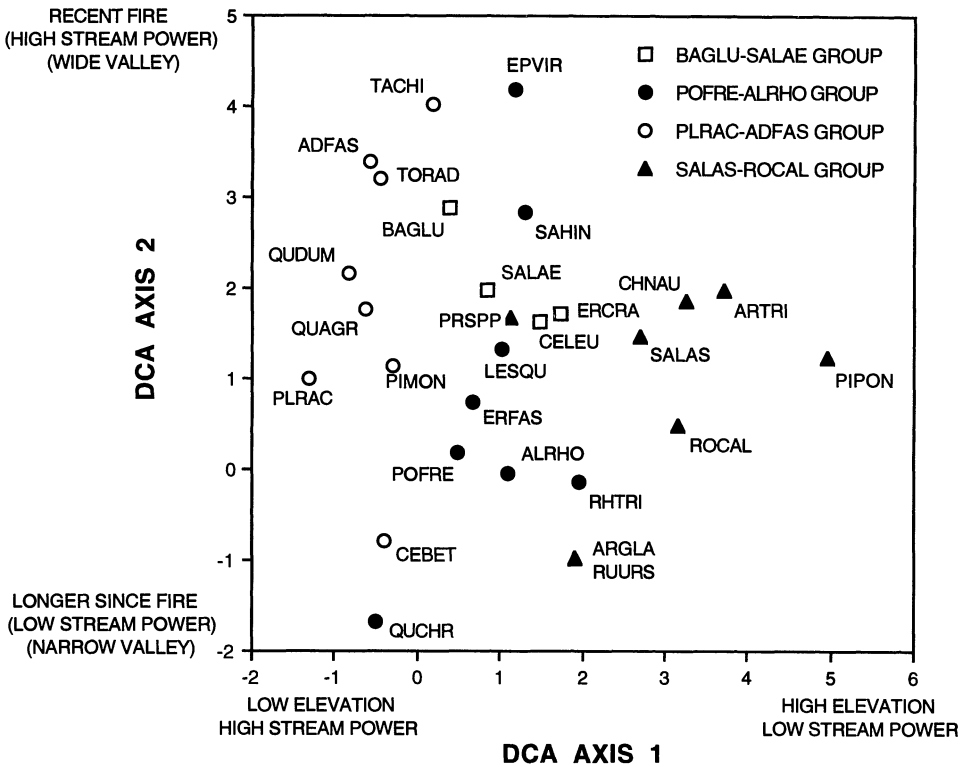


FIG. 4.—DCA ordination diagram of species, by TWINSpan group. Explanatory variables from equations 2 and 3 that are not directly correlated with axis scores are in parentheses. Species acronyms are listed in Table 4

fits with Hanes *et al.*'s (1989) description of *Baccharis glutinosa* as a pioneer species after flooding, and the prominence of *B. glutinosa* and presence of *Eriodictyon crassifolium* (another group member) within 2 yr after fire at a site studied by Davis *et al.* (1989). Both species are physiologically suited to maintaining their presence in the face of both fire and destructive floods, as they produce sprouts from stump or root after burning or cutting (Conrad, 1987).

Baccharis glutinosa is said to become prominent in the place of *Salix hindsiana* (which was not classified in the *Baccharis*/*S. laevigata* group) where conditions are too xeric for

TABLE 3.—TWINSpan site group means \pm standard deviations of environmental variables included in the regression models predicting DCA site axis scores.

Variable	Group 1	Group 2	Group 3	Group 4
Elevation	960 \pm 158	1082 \pm 148	952 \pm 136	1257 \pm 174
Fire	35 \pm 25	54 \pm 29	65 \pm 31	38 \pm 27
Mean 20-yr stream power	1750 \pm 2383	1518 \pm 890	1850 \pm 1596	708 \pm 1169
Valley bottom width	97 \pm 45	89 \pm 62	123 \pm 86	178 \pm 86

TABLE 4.—Species names, by groups, with acronyms, mean relative cover, and maximum relative cover at any site

Scientific name	Acronym	Mean rel. cover (%)	Max. rel. cover (%)
<i>Salix lasiolepis</i> / <i>Rosa californica</i> group			
<i>Salix lasiolepis</i> Benth.	SALAS	25.0	100.0
<i>Rosa californica</i> Cham. and Schlecht	ROCAL	4.8	35.7
<i>Artemisia tridentata</i> Nutt.	ARTRI	1.1	21.0
<i>Chrysothamnus nauseosus</i> (Pall.) Britton	CHNAU	0.8	11.0
<i>Pinus ponderosa</i> Dougl. ex P. and C. Lawson	PIPON	0.8	25.3
<i>Arctostaphylos glauca</i> Lindl.	ARGLA	0.3	9.6
<i>Prunus</i> spp.	PRSPPP	0.2	6.5
<i>Rubus ursinus</i> Cham. and Schlecht	RUURS	0.1	3.5
<i>Populus fremontii</i> / <i>Alnus rhombifolia</i> group			
<i>Populus fremontii</i> Wats.	POFRE	16.5	73.0
<i>Alnus rhombifolia</i> Nutt.	ALRHO	11.9	61.0
<i>Salix hindsiana</i> Benth.	SAHIN	8.4	43.6
<i>Lepidospartum squamatum</i> (Gray) Gray	LESQU	4.2	33.9
<i>Eriogonum fasciculatum</i> Benth.	ERFAS	1.3	11.5
<i>Ephedra viridis</i> Cov.	EPVIR	1.0	32.0
<i>Quercus chrysolepis</i> Liebm.	QUCHR	0.6	10.4
<i>Rhus trilobata</i> Nutt. ex T. and G.	RHTRI	0.2	5.4
<i>Baccharis glutinosa</i> / <i>Salix laevigata</i> group			
<i>Salix laevigata</i> Bebb.	SALAE	8.0	35.2
<i>Baccharis glutinosa</i> Pers.	BAGLU	6.0	48.2
<i>Eriodictyon crassifolium</i> Benth.	ERCRA	1.0	11.3
<i>Ceanothus leucodermis</i> Greene	CELEU	0.9	18.1
<i>Platanus racemosa</i> / <i>Adenostoma fasciculatum</i> group			
<i>Platanus racemosa</i> Nutt.	PLRAC	2.8	33.8
<i>Adenostoma fasciculatum</i> H. and A.	ADFAS	1.1	22.1
<i>Cercocarpus betuloides</i> Nutt. ex T. and G.	CEBET	0.9	19.8
<i>Toxicodendron radicans</i> L. ssp. <i>diversiloba</i> (T. and G.) Thorne	TORAD	0.8	16.4
<i>Quercus dumosa</i> Nutt.	QUDUM	0.7	16.3
<i>Tamarix chinensis</i> Lour.	TACHI	0.5	12.6
<i>Pinus monophylla</i> Torr. and Frem.	PIMON	0.2	7.4
<i>Quercus agrifolia</i> var. <i>frutescens</i> Engelm.	QUAGR	0.1	2.0

the latter species (Holstein, 1984). This would accord with the low elevation of these sites, in view of the considerable decrease in precipitation with decreased elevation in these mountains (Barbour, 1988). Zimmerman (1969) concluded that in many dry riparian environments plants are dependent on soil moisture stored from precipitation, rather than surface or ground water. Relative cover of *B. glutinosa* at sites in the study area is, in fact, significantly and negatively correlated with elevation ($r = -0.39$).

There has been little research on the autecology of *Salix laevigata*, but Holstein (1984) observed that this is among the more drought-adapted willows, which would be an advantage if these low-elevation sites are quite xeric. Such potentially xeric conditions, along with fire history, may be important in explaining the presence of *Ceanothus leucodermis*, which

TABLE 5.—Mean relative cover of the two most common species from each TWINSpan species group within each TWINSpan site group

Species	Group 1	Group 2	Group 3	Group 4
<i>Baccharis glutinosa</i>	16.1	3.2	1.8	0.5
<i>Salix laevigata</i>	18.3	6.6	1.5	1.8
<i>Populus fremontii</i>	15.4	34.2	14.1	3.6
<i>Alnus rhombifolia</i>	4.8	22.4	21.8	6.9
<i>Platanus racemosa</i>	0.0	3.1	21.1	0.0
<i>Adenostoma fasciculatum</i>	3.8	0.0	0.0	0.0
<i>Salix lasiolepis</i>	12.9	15.6	3.0	51.1
<i>Rosa californica</i>	0.0	4.3	0.0	11.3

is generally associated with dry slopes (McMinn, 1939), in this group. *Ceanothus leucodermis* is a chaparral species, and capable of regeneration by both seeding and sprouting after fires (Keeley and Keeley, 1988).

The *Populus/Alnus* group was linked with site group 2, which was characterized by high stream power, plus longer time since burning and higher elevations than group 1. All three of these environmental conditions logically favor *Alnus rhombifolia*. It is apparently flexible enough to survive severe floods, and indeed is the only common species in the data set that is significantly correlated with stream power ($r = 0.41$). *Alnus rhombifolia* does not recover swiftly after burning; Davis *et al.* (1989) found that it sprouted poorly and produced few viable seeds in a burned riparian reach, whereas its seedlings were common in an unburned reach immediately downstream. To the extent that higher elevations are more mesic, this factor may also contribute to explaining the distributional pattern of *A. rhombifolia* in the watersheds. *Alnus rhombifolia* has been particularly noted for its relatively high moisture requirements (Brothers, 1985; Parikh, 1989).

Populus fremontii may be another species favored by mesic high elevation conditions, as it is described as requiring moist sites (Rich and Borchert, 1982). The presence of *P. fremontii* and of *Eriogonum fasciculatum* within this group reflects only relative abundance, however, as they were observed at most of the study sites. Among other members of the *Populus/Alnus* species group, *Quercus chrysolepis* is described as being very sensitive to fire (Rich and Borchert, 1982), and though it is capable of sprouting after fires, this sensitivity may account for its presence in this group, along with the narrow valleys typical of group 2 sites. The preferential occurrence of this species in narrow valleys is reflected both in range descriptions (Rich and Borchert, 1982) and in its common name: canyon oak. *Lepidospartum squamatum* is frequently reported to prefer alluvial surfaces (McMinn, 1939; Smith, 1980; Hanes *et al.*, 1989), but without physiological explanation for this affinity. It may be present here as an effective colonizer after destructive floods; Hanes considers it to be a reliable indicator of flood-disturbed sites (pers. comm., 1991). The presence of *Salix hindsiana* within this high stream power habitat is in keeping with many discussions of its ecological role, in which it is invariably described as a post-flood riparian pioneer species (Holstein, 1984; McBride and Strahan, 1984a, b; Harris, 1987).

The *Salix lasiolepis/Rosa* group is associated with group 4, with high elevation and low stream power sites. Elevation is the probable key for at least some of the taxa in this species group. Relative cover of both *Salix lasiolepis* and *Rosa californica* is positively correlated with elevation ($r = 0.56$ and $r = 0.46$, respectively). The inclusion of *Pinus ponderosa* in this group accords with Barbour's (1988) observation that the species is limited to the highest

elevations in the Transverse Ranges, possibly due to moisture requirements. *Artemisia tridentata* and *Chrysothamnus nauseosus* may be here due to the low stream power at these sites. Neither is a true riparian species, and their weak rooting and brittle limbs can hardly be well-adapted to withstanding severe floods.

The *Platanus/Adenostoma* group is not amenable to simple explanations, as the group does not accord well with any of the site groups, and the individual species did not appear at enough sites for statistically meaningful correlations with environmental variables. While axis positions in the ordination diagram are a weak indicator, *Adenostoma fasciculatum*, *Quercus dumosa*, *Quercus agrifolia* and *Toxicodendron radicans* all appear high on the second DCA axis, indicative of recent fire. All are species common to (relatively) mesic chaparral (Keeley and Keeley, 1988). The recency of fire indicated by these high scores on Axis 2 are in keeping with the environmental and disturbance affinities of these nonriparian elements (Minnich and Howard, 1984).

One other member of the *Platanus/Adenostoma* group has an apparent rationale for its distribution. *Tamarix chinensis* occurred only at sites within group 1, a low elevation group. This position for *T. chinensis* probably relates to the geography of its spread, rather than a particular preference for that elevation. The species was found at low sites on Piru Creek because these were close (within 3 km) to Pyramid Reservoir. Major concentrations of *Tamarix* occur preferentially on the margins of reservoirs (Robinson, 1965; Harris, 1966).

Overall, elevation emerges as a prominent among-site variable in accounting for species/environment relations observed in southern California riparian habitats. This is hardly surprising, as steep lapse rates of precipitation and temperature are common in this environment (Barbour, 1988). To the extent that these control the availability of moisture and energy, they are likely to exert an overarching control on vegetation. It is only within the elevational ranges of component species that other variables can be expected to assume importance in explaining their distribution.

The other variables that are important in describing distributional patterns in these riparian settings are both agents of disturbance: stream power and fire. Again, their prominence is logical. Where disturbance occurs, there must be some impact on the vegetation, whether the impact is directional in the Clementsian (1916) sense, or less orderly and predictable, as described by Egler (1954). The riparian environment is defined (for this study, at least) by floods, and thus some flood impacts are inevitable. Similarly, the study was performed in a region where fire is frequent and nearly ubiquitous (Minnich and Howard, 1984). Little of the riparian environment along Piru and Sespe creeks is sufficiently mesic to preclude fire, so it has as much potential for an ecological role here as on the surrounding hillslopes. Valley width (included in equation 3) may influence the distribution of stream power in a more subtle way than was captured by stream power variance, which did not enter the model as a variable. This could, for example, be related to the tendency of the streams to occupy multiple, braided channels in the wider reaches.

The failure of aspect to influence vegetation at these sites probably reflects the fact that any given site has two opposing slopes, whose impact is canceled when vegetation data are summed across the site. Brothers (1985) found a significant role for downvalley aspect, the measure used here. Perhaps this reflects the placement of his sites in smaller streams than in the present study; within Brothers' narrow, low-order tributary canyons, shading was probably a more important factor.

The nonsignificant role of livestock in these analyses may simply reflect rather light grazing pressure. The effects of cattle were not obvious in the field: no streambanks were trampled, and no browse line was visible on the vegetation. The dichotomous variable used for grazing may be obscuring the fact that even the grazed sites have not been heavily stocked,

so that they are not prime examples of livestock use. These results should not, therefore, be generalized to conclude that grazing has no impact on riparian vegetation. In fact, the limited grazing history of the study area (relative to most western U.S. watersheds) has been a factor in recent consideration of these streams for classification as protected wild and scenic rivers.

In general, the riparian vegetation in this area responds to several of the environmental variables measured in the study. These results do, however, indicate the need for caution in interpreting species distributions. Harris (1987) suggested that the inverse of a flood disturbance gradient was a successional gradient, with pioneer species at the most disturbed points, etc. Such an interpretation may be an oversimplification of ecological reality. This study does suggest a major role for disturbance. But the overall distribution of species indicates a complex interaction of environmental factors with different importance to different species. Clearly, elevation, fire history, stream power and valley width are environmental variables accounting for much of the variation in species composition measured in this study. The variety of species responses to these environmental variables, however, suggest an interpretive posture that emphasizes the individualistic nature of species assemblages. At any given site, overall composition reflects the cumulative effect of species responding in different ways and to different variables, rather than in a synchronized, communal manner (Gleason, 1926). This range of individualistic responses does not fit neatly into a disturbance-succession framework.

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