

Scale, Direction, and Pattern in Riparian Vegetation-Environment Relationships



Jacob Bendix

Annals of the Association of American Geographers, Vol. 84, No. 4. (Dec., 1994), pp. 652-665.

Stable URL:

<http://links.jstor.org/sici?sici=0004-5608%28199412%2984%3A4%3C652%3ASDAPIR%3E2.0.CO%3B2-X>

Annals of the Association of American Geographers is currently published by Association of American Geographers.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/aag.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact support@jstor.org.

Scale, Direction, and Pattern in Riparian Vegetation-Environment Relationships

Jacob Bendix

Department of Geography, Maxwell School of Citizenship and Public Affairs, Syracuse University

Considerations of scale are central to the geographic analysis of natural phenomena in general, and to biogeography and ecology in particular (Meentemeyer and Box 1987; Meentemeyer 1989). Having acknowledged scale's effects on vegetation patterns (O'Neill et al. 1991), environmental scholars are trying to clarify the ways in which these patterns—and the environmental relationships creating them—change across geographical scales (Baker 1989; Levin 1992). Much of this work has been tied to hierarchy theory which holds that processes at a given scale exercise at least partial control over processes operating at larger map scales (i.e., over smaller areas) (Allen and Starr 1982; O'Neill et al. 1986; Urban et al. 1987). Baker (1989) has cautioned, however, that environmental influences are not invariably hierarchical. This paper suggests that a non-hierarchical approach to scalar comparisons may afford a clearer view of environmental relationships operating at different scales. The paper then evaluates the effects of these non-hierarchical, multi-scale environmental relationships on vegetation patterns in riparian environments of southern California.

Hierarchical and Non-hierarchical Environmental Relationships

Hierarchy theory implies a deterministic relationship between environmental processes operating at different scales. More precisely, processes operating at small map scales (large area) serve as constraints on processes operating at large map scales because the former define the environmental conditions within which the latter occur (Allen and Starr 1982).

Hierarchy theory further implies that environmental features as well as processes are hierarchically linked at successive scales. In riparian settings, the hierarchical model seems quite appropriate for some variables. The small map-scale variable of drainage area, for instance, exerts a measure of control over larger map-scale variables such as discharge, flow dimensions, and velocity (Leopold and Maddock 1953; Leopold and Miller 1956). Conversely, other small map-scale variables (e.g., elevation or soil nutrients), though they may be covariant with larger map-scale hydrologic variables, probably do not exert hierarchical influence on them. This distinction is crucial: Some scale relationships involve hierarchically linked causal sequences, while others are merely covariant, that is, they are functionally unrelated. While the hierarchical relationships depicted in Figure 1 may be more complex than this simple version (i.e., there could be many more arrows, directed sideways as well as downward), this simple linear version illustrates the central point, namely that some variables are controlled by processes that operate over larger areas.

The distinction between hierarchical and non-hierarchical interactions is important insofar as it facilitates analysis of the effects of different scale processes on vegetation patterns. Analysis of the effects of seemingly unrelated environmental factors at various scales may reveal significant influences on vegetation patterns. If small-scale factors (variable A, Figure 1) are most important, then the resulting vegetation pattern should exhibit a coarse texture, with large areas of homogeneous vegetation. If, however, the vegetation is dominated by large-scale factors (variable C, Figure 1), the vegetation pattern will exhibit a fine texture. These distinctions and their significance for the

Hierarchical and Non-Hierarchical Scale Relationships

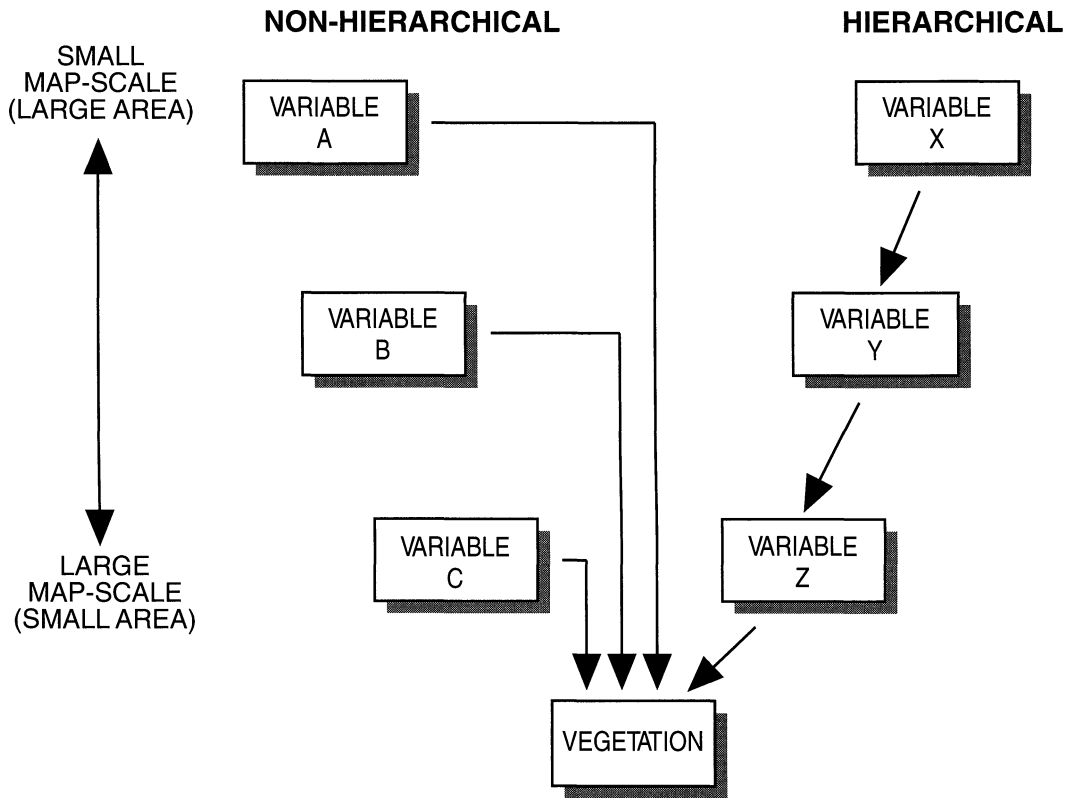


Figure 1. Hierarchical and non-hierarchical scale relationships.

vegetation pattern are obscured, however, by hierarchical relations in the environmental factors.

When environmental variables are hierarchically linked, smaller-scale environmental factors influence vegetation indirectly via their control of variables operating at larger scales. The vegetation pattern, of course, will reflect the environmental factors that are directly affecting the plants (variable Z, Figure 1). Since these assumptions preclude the emergence of vegetation patterns at other scales, environmental variables at other scales (variables X and Y, Figure 1) can have no direct effects on vegetation.

Regarding the role of scale as problematic, this paper explores the development of vegetation patterns in response to environmental

variations at contrasting scales. As the preceding discussion suggests, such a comparison would be futile in a hierarchical context; accordingly, the ensuing analysis is explicitly non-hierarchical and thus avoids the inclusion of variables that are functionally related to one another.

Scale and Pattern in Riparian Environments

Riparian environments provide a distinctive setting for comparing vegetation patterns produced by responses to environmental variables at different scales. Because of the linear nature of these environments, scale and direction co-

vary. Valley bottoms have two distinct spatial axes: 1) longitudinal or up- and down-valley; and 2) transverse or across the valley (Malanson 1993). The former is evident at small map scales, typically on a scale of kilometers, and the latter at large map scales, typically on a scale of meters (Figure 2). This interleaving of direction and scale suggests that the dominant scale of environmental influence will influence not just the texture of the resultant vegetation pattern, but its orientation as well. If the dominant influence is exerted by longitudinal-scale variables, then the pattern will exhibit a down-valley tiered sequence of relatively homogeneous vegetation segments (Figure 3a). At the other extreme, if transverse-scale variables dominate, the vegetational pattern will exhibit a cross-valley sequence that is repeated from site to site, that is, an overall pattern of long, narrow compositional strips parallel to the stream (Figure 3b).

As Baker (1989) has demonstrated, the relative influence of scale (and associated environmental variables) on the composition of riparian vegetation varies spatially. But Baker's analysis, unlike the one conducted here, focuses on smaller scale processes. He compares "macro-scale" factors that vary between watersheds

with "micro-scale" factors that vary between cross sections. Baker's comparison of scalar interactions across multiple watersheds sets the stage for further analyses which examine scalar influences within watersheds. Because the scales analyzed here differ somewhat from those considered by Baker (1989), the distinctions should be kept clear: the "longitudinal-scale" variables in this analysis, which vary between cross sections in a given watershed, are thus equivalent to Baker's "micro-scale" terminology; the "transverse-scale" in this study represents a larger map scale that has no equivalent in Baker's analysis.

This study, then, offers a non-hierarchical evaluation of the roles of scale-specific environmental factors in shaping the pattern of riparian vegetation composition. Toward that end, the study of watersheds which exhibit significant variation in longitudinal- and transverse-scale factors permits an examination of the interplay of these scale effects on vegetation.

Methods: Study Area and Sources of Data

Study Area

The adjacent watersheds of Piru and Sespe creeks in the Transverse Ranges of southern California serve as the study area for this paper (Figure 4). These watersheds represent a "natural laboratory" of sorts. Located entirely within the Los Padres National Forest, the study area differs from many western riparian settings in that the impacts of livestock grazing on riparian vegetation have been minimal (Bendix 1994). Moreover, all sites lie upstream from flood- or sedimentation-control structures, thus ensuring that streamflows are unregulated. The lack of significant modification by grazing and the absence of flow regulation facilitates the assessment of "natural" interactions in these watersheds.

The climate is Mediterranean (Figure 5). Vegetation outside of the valley bottoms is predominantly chaparral species (Keeley and Keeley 1988), save for the highest elevations where ponderosa pine are prominent. Wildfires are common (Minnich 1983). Forest Service records reveal that many of the sites

Contrasting Riparian Spatial Axes

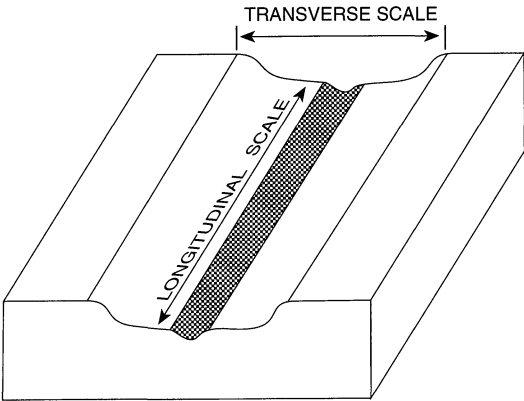


Figure 2. Longitudinal and transverse spatial axes of the riparian environment.

Potential Vegetation Patterns Reflecting Dominance of Environmental Variables Along a Single Axis

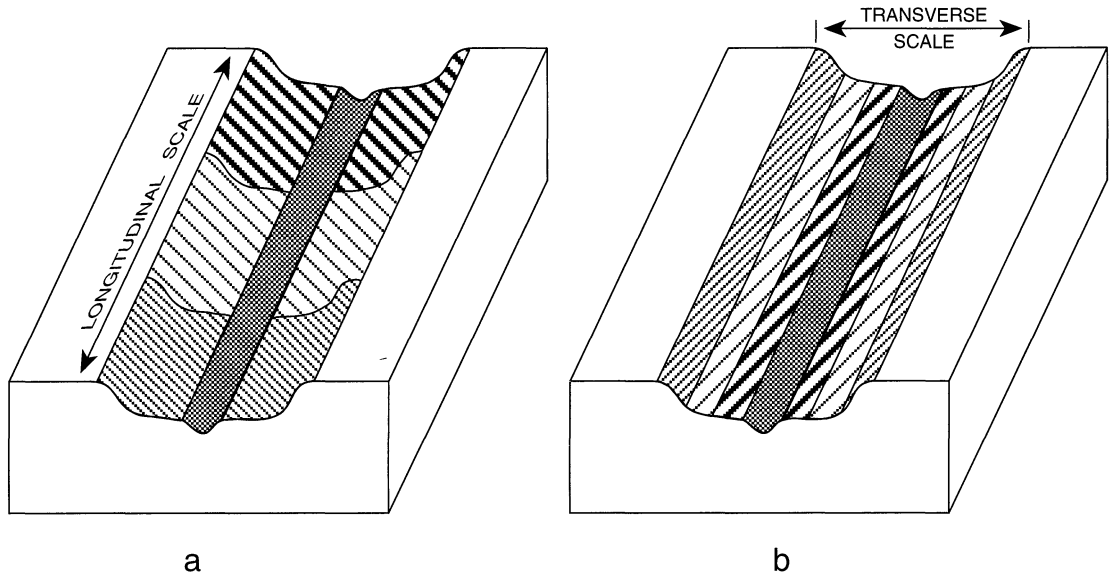


Figure 3. Potential vegetation patterns resulting from dominance of longitudinal-scale (a) or transverse-scale (b) environmental variables. Striping patterns represent different combinations of species.

have burned since 1910 (the first year of record). Site elevations range from 800 to 1450 meters.

Field Data Collection

More specifically, the analysis focuses on 17 valley bottom cross sections along Piru Creek and 20 cross sections in the Sespe watershed (Figure 4). These cross sections were located so as to ensure 1) regular spacing through the watersheds; 2) a range of cross-section shapes and orientations; and 3) minimal disruption by human artifacts such as road embankments. The field routine involved the use of line intercept sampling (Canfield 1941) and tabulation of the position and cover of woody species across each cross section. Each species occurring within a cross section is noted, along with the extent and location of the species within the cross section. Cross-sectional topography is surveyed using an automatic level, rod, and

tape; substrate variations along each cross-section are estimated visually; and the predominance of sand, cobble, boulder, or bedrock (the finest texture encountered was silty sand) is recorded.

Environmental Variables

I collected data on eight transverse and longitudinal variables that appear in the literature on riparian vegetation. Given the non-hierarchical approach of this study, I excluded certain longitudinal-scale variables that describe watershed characteristics (e.g. basin size, ruggedness) because their effects on vegetation are largely mediated by variables at subordinate scales.

Transverse-Scale Variables. The potential determinants of transverse variation in vegetation include: 1) distance above the water table; 2) flood severity; and 3) substrate texture (Frye

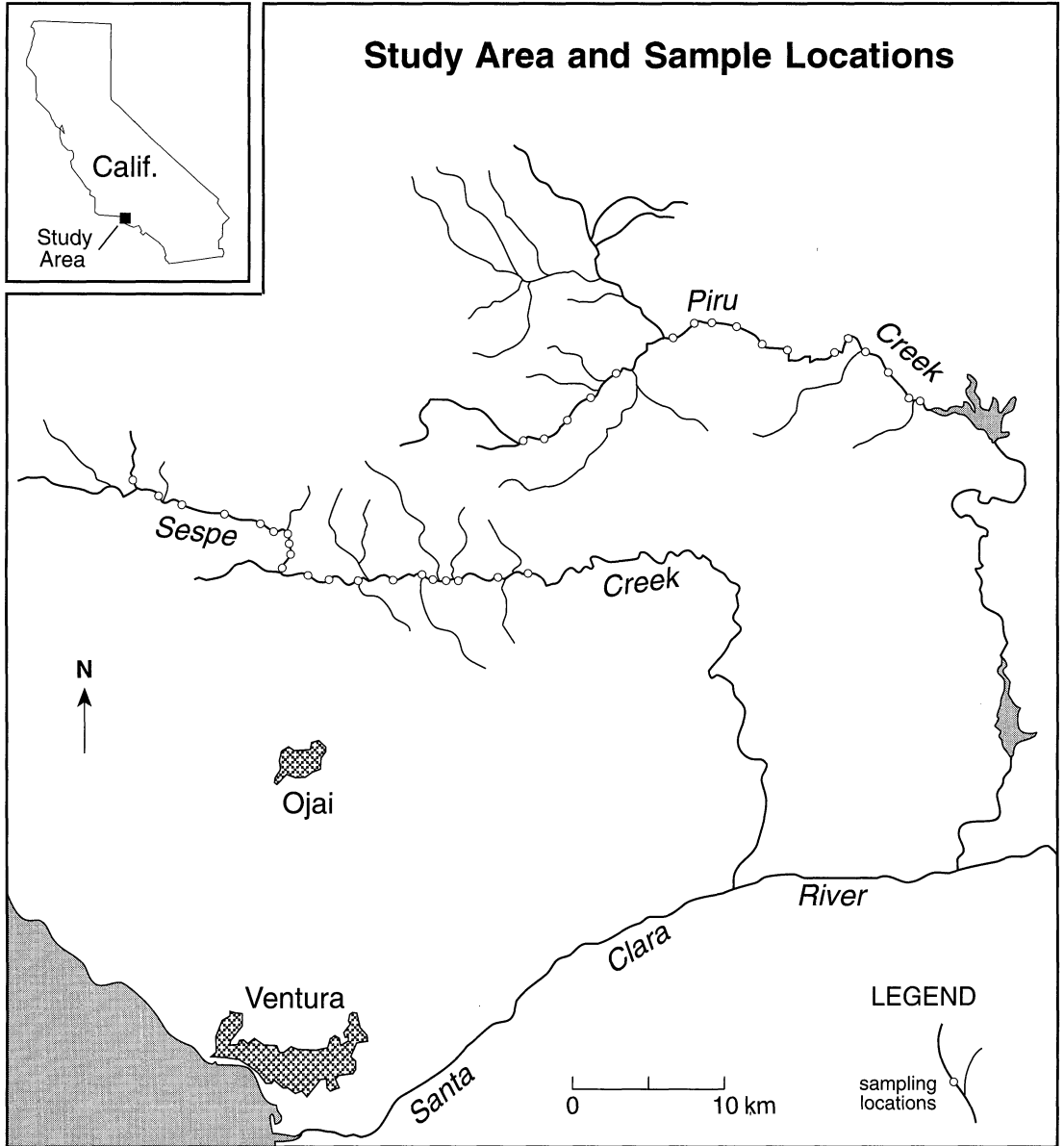


Figure 4. Sespe and Piru Creeks, California: Study area and sampling locations.

and Quinn 1979; Smith 1980; Hupp and Osterkamp 1985; Harris 1987; Bendix 1992). Their effects are rather well-known. Water-table distance may segregate vegetation because species differ in their rooting depths. Flood severity may sort species according to their fragility and their ability to colonize ground that has

been cleared by floodwaters. Substrate texture influences the availability of capillary moisture, and thus may affect species via their variable moisture requirements.

All of these transverse-scale variables may vary considerably within a given cross section. In order to capture that variability, each cross

Ojai Climograph

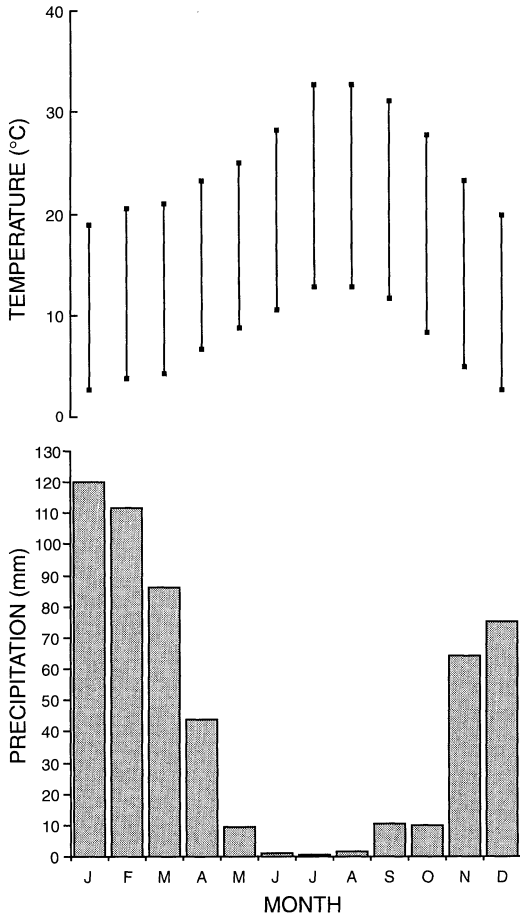


Figure 5. Climograph for Ojai, nearest climate station to the study area. Source: Monthly means for 1948–1986, National Climatic Data Center (1987).

section is further divided into four-meter linear segments; these are the units of observation. The value recorded for each of these segments represents the mean value of the variable within the four-meter segment. The endpoints of each cross section are determined by hydrologic calculations (described below) of the boundaries of the 20-year flood.

Distance above the water table is measured by the surrogate of the elevational difference

between the segment and the channel bed (Gordon et al. 1992); this is calculated from cross-section survey data.

The measure of flood severity is more complex. Severity is measured by unit stream power or the power exerted by flowing water per unit area of the surface that it passes over. This measure, unlike the closely related total stream power, varies within a cross section (Bagnold 1966; 1977; Costa 1983; Baker and Costa 1987). Unit stream power is defined by:

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

where ω equals unit stream power in watts per square meter (W/m^2); γ equals the specific weight of the fluid in Newtons per cubic meter (N/m^3); D equals depth of flow in meters (m); S equals the energy slope of the flow (a dimensionless term: m/m); and v equals flow velocity in meters per second (m/s). The derivation of values for these variables is elaborated below and in greater detail elsewhere (Bendix 1992).

In the calculation of unit stream power, I use a constant value of $9800 \text{ N}/\text{m}^3$ for γ (following Costa 1983; Baker and Costa 1987). The other variables, D , S and v , are all derived using the HEC-2 computer program (Feldman 1981; Hydrologic Engineering Center 1991). The latter requires four inputs: 1) survey data describing the valley's cross-section morphology; 2) an initial estimate of S to begin the iterative routine; 3) discharge; and 4) Manning's roughness coefficient (n) which measures frictional resistance to flow.

The first of these—cross-section morphology—comes from the field surveys of the cross sections. The second—the initial slope estimates—is derived from measurements of channel slope on topographic maps, a reasonable proxy in the absence of data for water-surface slope (Costa 1983; Magilligan 1988). The third—discharge—is estimated using a procedure developed by the U.S. Army Corps of Engineers for watersheds in this region (1985). This procedure deploys the so-called rational method (Dunne and Leopold 1978), albeit with empirical modifications based on local data. The rational method is appropriate for this portion of southern California given the prominence of frontal storms, although it is less appropriate for many western watersheds with convective storm regimes which result in considerable variability in precipitation (Graf 1988).

The discharge estimates used in this study are for the 20-year flood-recurrence interval which are developed incrementally for subunits of the basin (Graf 1988). It is worth noting that recent versions of HEC-2 differ from earlier ones in their capacity to correctly incorporate input data describing horizontal variation of Manning's n across the floodplain and channel (Hydrologic Engineering Center 1988). This study calculates variations of n within each cross section based on procedures developed by Arce-ment and Schneider (1989).

The final input—substrate variations—is based on field observations of modal particle size (or bedrock exposure, in some instances)—one of the more prominent substrate characteristics influencing, directly or indirectly, riparian vegetation (McBride and Strahan 1984). Other potential substrate influences, such as nutrient availability and subsurface textural variation, are not included here.

Longitudinal-Scale Variables. Turning to longitudinal variables having the potential for direct influences on riparian vegetation, this study includes: 1) elevation; 2) valley orientation; 3) valley width; 4) fire history; and 5) lithology (Brothers 1985; Parikh and Davis 1986; Baker 1989; Barro et al. 1989; Parikh 1989; Bendix 1994). These variables are considered longitudinal in scale because they are generally invariant within any given cross section, but variant between cross sections.

A brief explanation of each of these variables is in order. Elevation presumably influences vegetation via the combined effects of precipitation and temperature on available moisture. Valley orientation and width affect solar energy receipt; fires alter species composition in the aftermath; and lithology influences groundwater availability. Although fire history and lithology might vary within a cross section, such outcomes are sufficiently rare as to warrant classifying them as longitudinal variables.

The first three of these longitudinal variables are measured on 1:24,000 USGS topographic maps. The fourth, valley orientation, converts the section's downvalley aspect to a scalar of potential solar exposure and heat load (Parker 1982). Fire histories, reconstructed from unpublished Forest Service records, are recorded as the number of years since the last burning of the cross section. These records cover an

80-year period and they are based on fire-fighters' reports and maps of fire boundaries. Cross-section lithology is based on geological maps at a scale of 1:24,000 (Dibblee 1979a; 1979b; 1985; 1987; n.d.a; n.d.b.). Because the lithology variable seeks to capture potential influences on subsurface water availability rather than surface characteristics, the cross sections mapped as Quaternary alluvium are recorded as equivalent to the adjacent lithologic unit on the presumption that it underlies the alluvium. Lithology falls into one of five general rock types—sandstone, shale, conglomerate, crystalline, and unconsolidated material. Lastly, note that the value assigned to a particular longitudinal variable is the same across all of the four-meter segments within a given cross-section.

Analysis: DCA, PCA, Regression and ANOVA

In sum, the analysis includes 37 cross sections divided into 404 four-meter segments. The three transverse-scale variables are calculated for each segment and the five longitudinal-scale variables are calculated for each cross section. Six of the environmental variables are continuous and two (substrate texture and lithology) are categorical. In one case, unit stream power, values are transformed to logarithms, because previous work has demonstrated a non-linear vegetational response to this transverse-scale variable (Bendix 1992; 1994).

The vegetation data are also assigned to the four-meter segments. These data are summarized by a single measure of the overall composition of the vegetation within each segment. This composite measure derives from detrended correspondence analysis (DCA) (using the CANOCO program, Ter Braak 1985). This descriptive ordination routine simplifies ecological datasets that contain multiple species (Hill and Gauch 1980). I omit species that appear in fewer than 1 percent of the 404 sample segments because inclusion of these rare species distorts scaling within the ordination. As in most ordinations, the first axis generated by DCA is the most effective in representing the overall variation within the original dataset. Accordingly, first axis sample scores

from this ordination serve as the dependent variable in ensuing analyses.

The first set of analyses tests the impact of the variously scaled environmental variables on vegetation using multiple regression. Because the analysis seeks to assess the importance of scale of variables rather than of the individual variables themselves, I use principal components analysis (PCA) with varimax rotation. PCA reduces the dimensionality of the six independent (environmental) variables with continuous measures. The axes (components) produced by PCA are then interpreted as representing transverse- or longitudinal-scale environmental variation; hence these axes are used as predictor variables in the regression model. The use of the PCA axes (which are constrained to be orthogonal to one another) has the additional advantage of avoiding multicollinearity among the independent variables. Because the purpose of the analysis is to compare the influence of different scale variables—and not to generate the “best” model of the vegetational data—all of the interpretable axes are included in the regression model.

Note that two of the independent variables, substrate (transverse-scale) and lithology (longitudinal-scale), are categorical and thus are not amenable to inclusion in the PCA and regression procedures. Their contribution to vegetation patterns is assessed subsequently using analysis of variance (ANOVA) that models the influence of these categorical variables on the regression residuals.

Statistical Outcomes

The dependent variable is derived from a detrended correspondence analysis that in-

cludes twenty-two species. The results of the DCA yield the descriptive measure of vegetation. The first DCA axis, with an eigenvalue of .926, accounts for 29.5 percent of the variance in the first four axes, or 6.6 percent of total species variance. These proportions, which represent the extent to which one axis describes the combined variation of 22 variables (the original data for the species), reflect the noisiness that is typical of ecological datasets (Ter Braak 1985).

Turning to the independent variables, the PCA ordination yields four rotated components with eigenvalues exceeding 1.0 (Table 1). The first component represents transverse-scale environmental variation, and both stream power and water-table height load on it. Subsequent components separate out the longitudinal-scale variables, with the second component representing valley width; the third, elevation and aspect; and the fourth, fire history.

In the regression model, all four of the rotated components (C1–C4) make significant contributions ($p < .05$) to the prediction of the DCA scores (as indicated by *t*-statistics for parameter estimates). Comparison of standardized coefficients indicates that the transverse-scale variables (component C1) are the largest contributors to the model:

$$\text{DCA} = 0.337(\text{C1}) - 0.242(\text{C3}) + 0.173(\text{C4}) + 0.105(\text{C2}) \quad (2)$$

This model accounts for 21 percent of the variance in DCA scores, and is significant at the .001 level. Given the noisiness of the initial dataset and the multiple steps of the analysis, this R^2 suggests the strength of the underlying relationships. Visual inspection of residual plots

Table 1. Rotated Factor Pattern for Components Comprised of Environmental Variables.

Variable	Component			
	1	2	3	4
Water Table Distance	0.958	-0.145	-0.024	0.058
Log ₁₀ (20-year power)	-0.783	-0.479	-0.059	0.251
Valley Width	0.030	0.939	-0.056	0.042
Elevation	0.003	0.448	0.741	-0.254
Aspect	0.009	-0.266	0.887	0.087
Fire	-0.056	0.012	-0.041	0.983
Eigenvalue	1.535	1.403	1.345	1.106
% variance explained	25.6	23.4	22.4	18.4

reveals homoscedasticity and minimal autocorrelation which are indicative of an unbiased and correctly specified regression model.

The relative contributions of scale are obscured somewhat by the fracturing of the multiple components representing longitudinal-scale variables. One way of assessing the contributions of longitudinal and transverse scales to explained variance in the total model is to sum Type III (or partial) sums of squares for the longitudinal-scale components in the model and compare that figure with the Type III sum of squares for the single transverse-scale component. This assessment reveals that although the transverse-scale variables explain the most variance, the combined contribution of the longitudinal-scale variables is almost as great (Table 2). The net result is that neither scale seems to exert dominance. This interpretation is reinforced by the ANOVA which demonstrates that both substrate (transverse) and lithology (longitudinal) exert small but significant ($p < .05$) impacts on the regression residuals' variation, that is, transverse and longitudinal variables jointly influence vegetation patterns.

Scalar Effects on Vegetation Patterns

The regression analysis of transverse- and longitudinal-scale variables, in which both contribute significantly, suggests that vegetation patterns reflect a subtle combination of overlapping gradients. In its geographic expression, this analysis implies the overlay of a down-valley vegetation pattern imposed by longitudinal-scale variables upon a cross-valley pattern imposed by transverse-scale variations in stream power and water-table depths. Vegetation thus constitutes a spatial mosaic, wherein the mix

of vegetation at any particular point represents a unique intersection of influences operating at different scales—and, consequently, in different directions (shown schematically in Figure 6).

The complexity of this mosaic reflects in part the presence of multiple species within the overall pattern. Correlation of species cover with the several rotated PCA components illustrates that the relationship varies by species (Table 3). But even these correlations do not reveal the complexity of the environmental interactions involved since the bivariate correlations cannot capture what are essentially multivariate relationships. Indeed, each species may respond to a different combination of transverse- and longitudinal-scale variables.

The superposition of different scaled patterns on each other is often taken as evidence of hierarchical organization. As O'Neill et al. (1991) point out, however, multiscale patterns

Potential Vegetation Influenced by Variables Along Both Axes

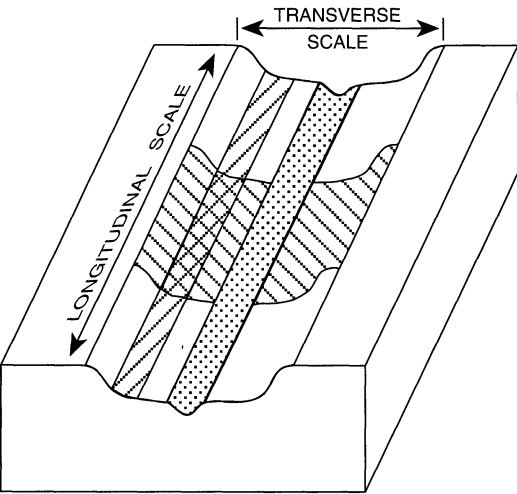


Figure 6. Schematic of vegetation pattern resulting from the intersection of transverse- and longitudinal-scale axes. As in Figure 3, striping patterns represent different combinations of species. The pattern at the intersection reflects the combination of environmental influences that operate on each scale, and thus represents a combination of the vegetation patterns that would result from each.

Table 2. Comparison of Type III Sums of Squares for the Components Entered as Variables in the Regression Model.

Component	Type III sum of squares
Component 2	7.889
Component 3	41.642
Component 4	21.403
Sum for longitudinal components	70.934
Component 1	81.144

Table 3. Species in the Dataset Listed by the Components with which their Cover Values are most Strongly Correlated (nomenclature after Munz and Keck 1968).

Component	Species
1	<i>Alnus rhombifolia</i> Nutt. <i>Eriodictyon crassifolium</i> Benth. <i>Eriogonum fasciculatum</i> Benth. <i>Lepidospartum squamatum</i> (Gray) Gray <i>Salix Hindsiana</i> Benth. <i>Salix laevigata</i> Bebb.
2	<i>Adenostoma fasciculatum</i> H. and A. <i>Artemisia tridentata</i> Nutt. <i>Baccharis glutinosa</i> Pers. <i>Cercocarpus betuloides</i> Nutt. ex T. and G. <i>Ephedra viridis</i> Cov. <i>Platanus racemosa</i> Nutt. <i>Toxicodendron radicans</i> L. ssp. <i>diversiloba</i> (T. and G.) Thorne <i>Tamarix chinensis</i> Lour.
3	<i>Chrysothamnus nauseosus</i> (Pall.) Britton <i>Pinus ponderosa</i> Dougl. ex P. and C. Lawson <i>Quercus dumosa</i> Nutt. <i>Salix lasiolepis</i> Benth.
4	<i>Ceanothus leucodermis</i> Greene <i>Populus Fremontii</i> Wats. <i>Quercus chrysolepis</i> Liebm. <i>Rosa californica</i> Cham. and Schlecht

are non-hierarchical if these result from independently operating abiotic factors. The latter appears to be the case in these southern California valleys, where both our conceptual understanding of the variables and the orthogonality imposed on them by PCA attest to their independence.

Temporal Influences on Riparian Vegetation

The unexplained variance in the preceding model may be due, in part, to the role of other spatial variables that were excluded from the model. Many of these variables may operate at scales that are larger or smaller than those considered here (Baker 1989; Parikh 1989). It is

more likely, however, given this study's emphasis on spatial variables, that much of the unexplained variance in the model reflects the uncertain role of temporal succession (Malanson and Butler 1991). The importance of succession is underlined by the prominence of stream power and fire in the model, both of which are agents of disturbance. Clearly, disturbance and succession are inextricably entwined in the processes that produce spatial patterns in vegetation (White 1979), but even these agents do not fully encompass the temporal dimension. Singular historical events may also result in partial disequilibria between vegetation and environmental conditions (Vale 1989; Baker 1990; Sprugel 1991; Parker 1993). Given the emphasis on spatial rather than historical variation (with the exception of fire history), this study's research design lends itself to the interpretation of process relationships that are short term and rapidly equilibrating. The fact that a significant portion of the vegetation variation in the study area can be explained by ahistorical measures attests that this riparian vegetation is in sufficient equilibrium for much of its pattern to be determined by ahistorical environmental factors.

Implications for Human Impacts on Riparian Vegetation

Although this study is set in valleys that have experienced minimal human impact, the results suggest that human activities elsewhere in the region may have had subtle effects on the pattern of riparian vegetation. The balance in the effects of longitudinal- and transverse-scale environmental determinants on vegetation pattern implies that even where human activities do not result in the overall reduction or increase of individual species, these activities may change the patterns in which species occur. Any environmental change that alters the variance of factors at one scale relative to those of another scale will affect the orientation and the texture of the vegetation mosaic.

Flow regulation is a case in point. Many southern California streams have dams along them (including Piru Creek, downstream from the study area), and more dams are in the planning stages. Dams reduce the magnitude and frequency of downstream floods (Williams and

Wolman 1984), and thereby decrease the role of unit stream power, an element of transverse-scale environmental variation. Insofar as the decreased importance of transverse-scale variables involves a relatively greater influence for longitudinal-scale variables, the probable result is a change in the vegetation pattern toward greater homogeneity at each cross section (Figure 3a). This appears to be the case in at least one dammed watershed nearby (Mark Borcherdt 1990).

Conversely, human-induced reduction in longitudinal-scale variability should increase the linearity of vegetation patterns. For instance, fire suppression policies in twentieth-century southern California have greatly altered the pattern of wildfire occurrence in the area (Minnich 1983). The net result is a change from frequent small fires to infrequent but larger fires. Because fire history represents longitudinal-scale variation, this change in fire distribution results presumably in a reduction of longitudinal environmental heterogeneity. Concurrently, large fires in chaparral watersheds tend to increase flood magnitudes—through their influence on vegetation and soils (Nasseri 1989)—thereby enhancing the importance of the transverse-scale variable stream power. Thus while longitudinal variability decreases, transverse impacts are increasing. Fire suppression therefore may have shifted slightly the mosaic toward the linear pattern seen in Figure 3b.

Methodological Implications: Scale and Environmental Heterogeneity

The sensitivity of vegetation to transverse- and longitudinal-scale factors means that the results of this (or any) study of scale closely reflect the particular scales chosen for analysis. Had the sampling been confined to a smaller portion of the watersheds, longitudinal-scale variance would have been reduced, and environmental factors at that scale would have figured less prominently in the results. Alternatively, if sampling in the study area had been more extensive, covering for example the distance from the first-order tributaries of Piru and Sespe creeks to the mouth of the Santa Clara River, the dataset would have encompassed far more transverse-scale variance; the impor-

tance of transverse-scale relationships, meanwhile, would have diminished relatively. The results are similarly constrained by the spatial resolution of environmental heterogeneity reflected in the longitudinal-scale environmental variables. Elevation provides an obvious example. Because this study was conducted in a mountainous environment, steep stream gradients assured a wide range for this longitudinal-scale variable. It is not surprising, therefore, that elevation made significant contributions to one of the components (C3) in the regression model. Had this study been conducted in a lowland watershed, there would have been less variation in elevation and the contributions of longitudinal-scale variation would have been reduced. These caveats serve as a reminder of scale effects on vegetation patterning, and, more generally, of the importance of context-sensitive interpretations of environmental patterns and relationships.

Conclusions

Riparian environments provide a distinctive setting in which to explore vegetation-environment relationships at contrasting scales. Because valleys are linear features, the scales at which these relationships operate may have a profound influence on vegetation patterns. The relative role of factors influencing vegetation at different scales can only be discerned, however, if they are not hierarchically linked. That is not to say that emphasis on non-hierarchical relationships rules out the presence of hierarchical organization in this environment, but rather that an analysis that explicitly avoids hierarchical relationships is more likely to clarify other aspects of the scale and spatial alignment of environmental relationships in riparian settings. In that regard, the results of this study suggest two points: 1) that multiple, non-hierarchical variables do operate at contrasting scales; and 2) that the balance between those scales plays a critical role in determining the texture and orientation of a vegetation pattern that includes transverse and longitudinal elements.

Acknowledgments

The research reported here was conducted while I was a doctoral student in the Department of Geog-

raphy at the University of Georgia. I thank Carol Liebler and Mark Cowell for assistance in the field, Steve Junak for aid in species identification, Mark Borchert for information and assistance, and Al Parker, Ron Mitchelson, and Frank Magilligan for suggestions regarding various aspects of data analysis. I thank the Vernacchia family for hospitality during fieldwork, and the University of Georgia Cartographic Services for help in preparing Figure 4. I am indebted to Al Parker, Tom Vale and Bill Baker for thoughtful critiques of earlier versions of this manuscript; thanks also to the three anonymous reviewers. This research was supported in part by the U.S. Forest Service and a Sigma Xi Grant-in-Aid of Research.

References

- Allen, T. F. H., and Starr, T. B. 1982. *Hierarchy: Perspectives for Ecological Complexity*. Chicago: University of Chicago Press.
- Arcement, G. J., and Schneider, V. 1989. *Guide for Selecting Manning's Roughness Coefficients for Natural Channels and Flood Plains*. United States Geological Survey Water Supply Paper 2339. Washington, D.C.: U.S. Government Printing Office.
- Bagnold, R. A. 1966. *An Approach to the Sediment Transport Problem from General Physics*. United States Geological Survey Professional Paper 422-I. Washington, D.C.: U.S. Government Printing Office.
- . 1977. Bed Load Transport by Natural Rivers. *Water Resources Research* 13:303–312.
- Baker, V. R., and Costa, J. E. 1987. Flood Power. In *Catastrophic Flooding*, ed. L. Mayer and D. Nash, pp. 1–21. Boston: Allen and Unwin.
- Baker, W. L. 1989. Macro- and Micro-Scale Influences on Riparian Vegetation in Western Colorado. *Annals of the Association of American Geographers* 79:65–78.
- . 1990. Climatic and Hydrologic Effects on the Regeneration of *Populus angustifolia* James Along the Animas River, Colorado. *Journal of Biogeography* 17:59–73.
- Barro, S. C., Wohlgemuth, P. M., and Campbell, A. G. 1989. Post-Fire Interactions Between Riparian Vegetation and Channel Morphology and the Implications for Stream Channel Rehabilitation Choices. In *Proceedings of the California Riparian Systems Conference*, pp. 51–53. General Technical Report PSW-110. Berkeley: Pacific Southwest Range Experiment Station, United States Department of Agriculture Forest Service.
- Bendix, J. 1992. Scale-Related Environmental Influences on Southern Californian Riparian Vegetation. Ph.D. Dissertation, Department of Geography, University of Georgia.
- . 1994. Among-Site Variation in Riparian Vegetation of the Southern California Transverse Ranges. *American Midland Naturalist* 132:136–151.
- Borchert, M. 1990. Personal Communication. Goleta, California.
- Brothers, T. S. 1985. Riparian Species Distributions in Relation to Stream Dynamics, San Gabriel River, California. Ph.D. Dissertation, Department of Geography, University of California, Los Angeles.
- Canfield, R. H. 1941. Application of the Line Intercept Method in Sampling Range Vegetation. *Journal of Forestry* 39:388–394.
- Costa, J. E. 1983. Paleohydraulic Reconstruction of Flash-Flood Peaks from Boulder Deposits in the Colorado Front Range. *Geological Society of America Bulletin* 94:986–1004.
- Dibblee, T. W., Jr. 1979a. *Geologic Map of the Lockwood Valley Quadrangle, California (1:24,000)*. United States Geological Survey (Preliminary) Open-file Report.
- . 1979b. *Geologic Map of the Topatopa Mountains Quadrangle, California (1:24,000)*. United States Geological Survey (Preliminary) Open-file Report.
- . 1985. *Geologic Map of the Wheeler Springs Quadrangle, California (1:24,000)*. Santa Barbara: Thomas W. Dibblee, Jr. Geological Foundation.
- . 1987. *Geologic Map of the Lion Canyon Quadrangle, California (1:24,000)*. Map No. DF-14. Santa Barbara: Thomas W. Dibblee, Jr. Geological Foundation.
- . n.d.a. *Black Mountain (1:24,000)*. Preliminary draft for a geologic map. Map on file at Los Padres National Forest Headquarters, Goleta, California.
- . n.d.b. *McDonald Peak (1:24,000)*. Preliminary draft for a geologic map. Map on file at Los Padres National Forest Headquarters, Goleta, California.
- Dunne, T., and Leopold, L. B. 1978. *Water in Environmental Planning*. San Francisco: W. H. Freeman and Company.
- Feldman, A. D. 1981. HEC Models for Water Resources System Simulation: Theory and Experience. *Advances in Hydrosience* 12:297–423.
- Frye, R. J., II, and Quinn, J. A. 1979. Forest Development in Relation to Topography and Soils on a Floodplain of the Raritan River, New Jersey. *Bulletin of the Torrey Botanical Club* 106:334–345.
- Gordon, N. D., McMahon, T. A., and Finlayson, B. L. 1992. *Stream Hydrology*. New York: Wiley.
- Graf, W. L. 1988. *Fluvial Processes in Dryland Rivers*. New York: Springer-Verlag.
- Harris, R. R. 1987. Occurrence of Vegetation on Geomorphic Surfaces in the Active Floodplain of a California Alluvial Stream. *American Midland Naturalist* 118:393–405.
- Hill, M. O., and Gauch, H. G., Jr. 1980. Detrended Correspondence Analysis, an Improved Ordination Technique. *Vegetatio* 42:47–58.

- Hupp, C. R., and Osterkamp, W. R. 1985. Bottom-land Vegetation Distribution Along Passage Creek, Virginia, in Relation to Fluvial Landforms. *Ecology* 66:670–681.
- Hydrologic Engineering Center. 1988. *Supplement to HEC-2 User's Manual*. Davis, California: United States Army Corps of Engineers.
- . 1991. *HEC-2 Water Surface Profiles User's Manual*. Davis, California: United States Army Corps of Engineers.
- Keeley, J. E., and Keeley, S. C. 1988. Chaparral. In *North American Terrestrial Vegetation*, ed. M. G. Barbour and W. D. Billings, pp. 165–207. New York: Cambridge University Press.
- Leopold, L. B., and Maddock, T., Jr., 1953. *The Hydraulic Geometry of Stream Channels and Some Physiographic Implications*. United States Geological Survey Professional Paper 252. Washington, D.C.: U.S. Government Printing Office.
- Leopold, L. B., and Miller, J. P. 1956. *Ephemeral Streams—Hydraulic Factors and their Relation to the Drainage Net*. United States Geological Survey Professional Paper 282-A. Washington, D.C.: U.S. Government Printing Office.
- Levin, S. A. 1992. The Problem of Pattern and Scale in Ecology. *Ecology* 73:1943–1967.
- Magilligan, F. J. 1988. Variation in Slope Components During Large Magnitude Floods, Wisconsin. *Annals of the Association of American Geographers* 78:520–533.
- Malanson, G. P. 1993. *Riparian Landscapes*. Cambridge: Cambridge University Press.
- Malanson, G. P., and Butler, D. R. 1991. Floristic Variation Among Gravel Bars in a Subalpine River, Montana, U.S.A. *Arctic and Alpine Research* 23:273–278.
- McBride, J. R., and Strahan, J. 1984. Fluvial Processes and Woodland Succession Along Dry Creek, Sonoma County, California. In *California Riparian Systems*, ed. R. E. Warner and K. M. Hendrix, pp. 110–119. Berkeley: University of California Press.
- Meentemeyer, V. 1989. Geographical Perspectives of Space, Time and Scale. *Landscape Ecology* 3:163–173.
- Meentemeyer, V., and Box, E. O. 1987. Scale Effects in Landscape Studies. In *Landscape Heterogeneity and Disturbance*, ed. M. G. Turner, pp. 15–34. New York: Springer-Verlag.
- Minnich, R. A. 1983. Fire Mosaics in Southern California and Northern Baja California. *Science* 219:1287–1294.
- Munz, P. A., and Keck, D. D. 1968. *A California Flora with Supplement*. Berkeley: University of California Press.
- Nasseri, I. 1989. Frequency of Floods from a Burned Chaparral Watershed. In *Proceedings of the Symposium on Fire and Watershed Management*, pp. 68–74. General Technical Report PSW-109. Berkeley: Pacific Southwest Range Experiment Station, United States Department of Agriculture Forest Service.
- National Climatic Data Center. 1987. *TD 3200 Summary of the Day Cooperative Observer Network*. Denver: U.S. West Optical Publishing.
- O'Neill, R. V., DeAngelis, D. L., Waide, J. B., and Allen, T. F. H. 1986. *A Hierarchical Concept of Ecosystems*. Princeton, New Jersey: Princeton University Press.
- O'Neill, R. V., Turner, S. J., Cullinan, V. I., Coffin, D. P., Cook, T., Conley, W., Brunt, J., Thomas, J. M., Conley, M. R., and Gosz, J. 1991. Multiple Landscape Scales: An Intersite Comparison. *Landscape Ecology* 5:137–144.
- Parikh, A. K. 1989. Factors Affecting the Distribution of Riparian Tree Species in Southern California Chaparral Watersheds. Ph.D. Dissertation, Department of Geography, University of California, Santa Barbara.
- Parikh, A. K., and Davis, F. W. 1986. Terrestrial Vegetation of Rattlesnake Canyon. In *Proceedings of the Chaparral Ecosystems Research Conference*, ed. J. J. DeVries, pp. 13–17. Report No. 62. Davis: California Water Resources Center, University of California.
- Parker, A. J. 1982. The Topographic Relative Moisture Index: An Approach to Soil-Moisture Assessment in Mountain Terrain. *Physical Geography* 3:160–168.
- Parker, K. C. 1993. Climatic Effects on Regeneration Trends for Two Columnar Cacti in the Northern Sonoran Desert. *Annals of the Association of American Geographers* 83:452–474.
- Smith, R. L. 1980. Alluvial Scrub Vegetation of the San Gabriel River Floodplain, California. *Madroño* 27:126–138.
- Sprugel, D. G. 1991. Disturbance, Equilibrium, and Environmental Variability: What is 'Natural' Vegetation in a Changing Environment? *Biological Conservation* 58:1–18.
- Ter Braak, C. F. J. 1985. *CANOCO: A FORTRAN Program for Canonical Correspondence Analysis and Detrended Correspondence Analysis*. Wageningen, The Netherlands: IWIS-TNO.
- Urban, D. L., O'Neill, R. V., and Shugart, H. H., Jr. 1987. Landscape Ecology. *BioScience* 37:119–127.
- U.S. Army Corps of Engineers. 1985. Regional Floodflow Frequency Study, Calleguas Creek, Santa Clara and Ventura Rivers and Tributaries. In *Calleguas Creek Hydrology for Survey Report, Ventura County, California*, pp. 1–27 (Appendix 1). Los Angeles.
- Vale, T. R. 1989. Vegetation Management and Nature Protection. In *Natural Areas Facing Climate Change*, ed. G. P. Malanson, pp. 75–86. The Hague, The Netherlands: SPB Academic Publishing bv.

White, P. S. 1979. Pattern, Process and Natural Disturbance in Vegetation. *The Botanical Review* 45:229–299.

Williams, G. P., and Wolman, M. G. 1984. *Downstream Effects of Dams on Alluvial Rivers*. United

States Geological Survey Professional Paper 1286. Washington, D.C.: U.S. Government Printing Office.

Submitted 5/93, Revised 3/94, Accepted 5/94.

Bendix, Jacob. 1994. Scale, Direction, and Pattern in Riparian Vegetation-Environment Relationships. *Annals of the Association of American Geographers* 84(4):652–665. *Abstract.*

Because of the linear nature of riparian environments, direction and scale are closely linked. Cross-valley variation in mountain stream valleys is typically seen on a scale of meters, while variation up- and down-valley may be measured in kilometers. As a result, environmental factors at transverse scale (varying within a cross section) and at longitudinal scale (varying between cross sections) impose different patterns on vegetation. This paper compares these scale influences on the composition of woody riparian vegetation in southern California.

Using cover data from 37 valley cross sections in the Transverse Ranges, and dividing these into four-meter segments, I determine segment values for the longitudinal-scale variables of elevation, years since burning, aspect, valley width and lithology, and for the transverse-scale variables of water-table depth, unit stream power (for the 20-year flood), and substrate particle size. The influence of variables at these contrasting scales on the vegetation composition are compared using detrended correspondence analysis, principal components analysis, multiple regression, and analysis of variance. The results show that transverse- and longitudinal-scale variables have significant influences on the vegetation, though neither scale is dominant. All of which suggests that the complex mosaic of riparian vegetation in this environment reflects the coincidence of environmental relationships operating in different directions on contrasting scales. **Key Words:** California, fire, riparian vegetation, scale, stream power, vegetation-environment relationships.