

## Stream Power Influence on Southern Californian Riparian Vegetation

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# Stream power influence on southern Californian riparian vegetation

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**Abstract.** Mechanical damage by floodwaters is frequently invoked to explain the distribution of riparian plant species, but data have been lacking to relate vegetation to specific estimates of flood damage potential. This research uses detailed estimates of unit stream power (an appropriate measure of the potential for mechanical damage) in conjunction with vegetation cover data to test this relationship at 37 valley-bottom sites in the Transverse Ranges of Southern California. A computer program, HEC-2, was used to model the slope and the variation in flow depth and velocity of the 20-yr flood across the sites. Regression models tested the influence of stream power (and of height above the water table) on the woody species composition of 393 4-m cross-section segments of the valley-bottom sites. Results indicate that unit stream power does have a significant effect on the riparian vegetation, but that the amount of that influence and its importance relative to the influence of height above the water table varies between watersheds. Some species are found primarily in locations of high stream power, while others are limited to portions of the valley bottom that experience only low stream power.

**Keywords:** Detrended Correspondence Analysis; Disturbance; Flood; Transverse Ranges; Vegetation pattern; Water table.

**Nomenclature:** Hickman (1993).

## Introduction

The influence of flooding on species distributions has been a recurring topic in the study of riparian vegetation (e.g. Illichevsky 1933; McBride & Strahan 1984a, b; Hupp & Osterkamp 1985; Baker 1990; Carbiener & Schnitzler 1990; Bendix 1994a; Baker & Walford 1995; see Malanson 1993 and Parker & Bendix 1996 for reviews). Floods may exert such influence through transport of propagules, the imposition of anaerobic conditions in the root zone or through the direct mechanical work of floodwater in destroying vegetation or modifying substrates. Anaerobic effects are probably most important in environments where floodwaters remain at high levels for long periods (e.g. Hosner & Boyce 1962; Robertson et al. 1978), whereas mechanical impacts may be important in any environment where floods are of sufficient magnitude to damage plants or rework the surface on which they grow (e.g. Sigafoos 1961, 1964; Hupp 1982; Nilsson 1987).

While several studies have stressed the importance of the magnitude and frequency of mechanically effective floods in determining vegetation patterns (Hupp 1982, 1983; Osterkamp & Hupp 1984; Hupp & Osterkamp 1985; Harris 1987; Bornette & Amoros 1996), the potential for mechanical damage at any given location on the valley floor has generally been inferred from estimates of flood frequency. If vegetation is truly influenced by the mechanical work of floods, however, the energy exerted by the floods must be at least as important as the frequency of their occurrence. Among fluvial geomorphologists, stream power has been a favored measure of the energy required to do effective work (Bagnold 1966; Graf 1983; Miller 1990). Stream power refers to the amount of energy exerted by running water against the surfaces over which it flows. As such, it should reflect both the potential for direct impacts by moving water damaging vegetation and indirect impacts by floodwaters mobilizing sediment or large woody debris that may strike and damage vegetation (the size and quantity of material mobilized will be determined by the energy applied to that material). Baker & Costa (1987) have pointed out that the geomorphic effectiveness of floods is more dependent on shear stress and stream power per unit boundary area than on either magnitude or frequency. These measures of energy must similarly be important determinants of the mechanical impact of floods on vegetation.

The foregoing suggests that the influence of flooding on riparian vegetation can best be assessed by sampling vegetation in zones in which the stream power exerted by floods of varying recurrence intervals is known. Unfortunately, the data necessary for such an assessment rarely have been available. Harris (1987) noted the importance of stream power, but had to rely on the surrogate measure of sediment size, which reflects (in part) stream power, but does not indicate recurrence interval. Nilsson (1987) measured one of the components of stream power, velocity, but did so during low flows, rather than during floods, when most of the mechanical work of streams is done (Baker 1977; Wolman & Gerson 1978). Hupp (1982), Parikh (1989) and Bendix (1994a) did use various measures of stream power, but their measures were for entire valley bottom cross-sections.

In a given watershed, stream power will vary not only from one cross-section to another, but also (and perhaps more) within each cross-section (Bendix 1994b).

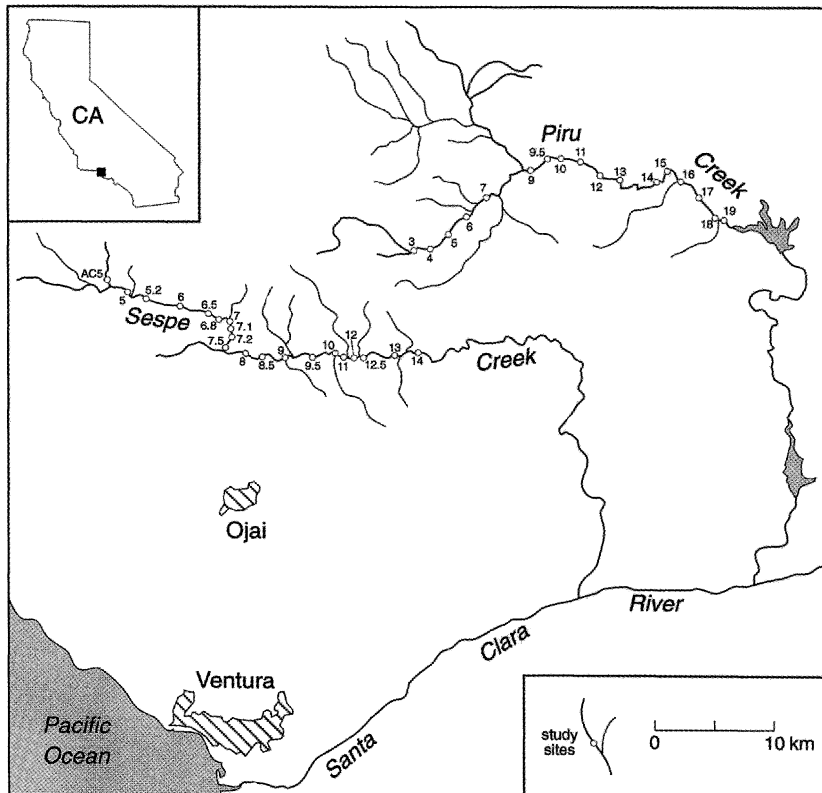
An additional factor complicating the assessment of flood impacts is the possible role of the water table in influencing riparian vegetation. With increasing height above the stream channel, the distance to the water table generally increases. This imposes a gradient of distance to water that may influence the valley-bottom vegetation (Frye & Quinn 1979; Parikh 1989). The absence of specific data on how stream power varies across the floodplain has made it particularly difficult to disentangle the roles of flood damage and height above the water table in determining riparian vegetation composition.

The purpose of this study was to develop quantitative estimates of the distribution of stream power, and use them to answer two questions: (1) does stream power have a measurable and significant influence on the distribution of riparian plant species; and (2) how does such influence relate to that of height above the water table, the other environmental variable that is related to valley bottom position. The second objective was included to avoid incorrectly attributing species' responses to moisture gradients as flood damage responses.

Studies that have related species occurrences to specific fluvial landforms have generally suggested that

these relationships reflect the varied flood impacts experienced on different landforms (Hupp & Osterkamp 1985; Harris 1987). The concentration on actual stream power, rather than landform position, in this analysis should provide a test of whether former does indeed provide a realistic mechanism for sorting vegetation on the latter. The riparian vegetation in the study area is clearly affected by a variety of environmental factors, not limited to the two analyzed here. Elevation, fire history and valley morphology all serve to differentiate the vegetation between one part of the watershed and another (Bendix 1994a). However, these environmental variables do not vary significantly at a given cross-section, and their influence can be distinguished both conceptually and quantitatively from those which do (Bendix 1994b). Only substrate characteristics are, like stream power and height above the water table, variable within individual cross-sections.

This research builds on previous work in the same setting which has established environmental relationships at the coarser, among-site scale (Bendix 1994a) and distinguished between the environmental influences applicable at different scales (Bendix 1994b); the intent of this paper is to focus specifically on the test of stream power influence at the finest resolution possible, while recognizing that it must be seen as occurring within a context of multiple influences.



**Fig. 1.** Map of study area and site locations (from Bendix 1994a).

## Methods

### Study area

Data were collected at the Piru and Sespe creeks (Fig. 1), adjacent watersheds in Ventura and Los Angeles counties, within Los Padres National Forest, in the upstream reaches of the streams where they flow through the Transverse Ranges, before emerging as tributaries into the Santa Clara River valley. Sampling on Piru Creek was conducted upstream of the dams on that stream; Sespe Creek is undammed. Piru Creek drains 510 km<sup>2</sup> at the lowest site within that watershed, and Sespe Creek drains 327 km<sup>2</sup> at its lowest site. Site elevations ranged from 800 m to 1450 m. This is a dry chaparral environment, with a mediterranean-type climate.

Steep hill slopes within the watersheds result in a 'flashy' hydrologic response to winter storms. Valley morphology on both streams varies from relatively open alluvial valley bottoms to rock-walled gorges (Fig. 2). The bedrock-controlled channels of the latter allow for very high values of stream power (Baker & Costa 1987); the alternation between these and alluvial reaches ensures that a range of flood impacts is represented. Channel patterns vary, with many compound channels (Graf 1988), a type which occupies a single channel at low flow but expands to a braided form with subchannels during high flows. Due to the range of valley and channel morphologies, distinct suites of landforms (cf. Hupp & Osterkamp 1985; Birkeland 1996) are rare; generally a given cross-section has one or two distinctly identifiable landforms (terraces, etc.), but the boundaries of others are imperceptible. These watersheds are unusual (for this region) in that livestock grazing is limited, with minimal impacts on the riparian vegetation (Bendix 1994a).

Prominent plant species in the riparian zone include *Alnus rhombifolia*, *Baccharis salicifolia*, *Platanus racemosa*, *Populus fremontii*, and some *Salix* species. These are mingled with representatives of the surrounding chaparral (dominated by *Arctostaphylos*, *Quercus* and *Ceanothus* species) and with *Pinus ponderosa* covering hill slopes at the highest altitude sites.

### Field data collection

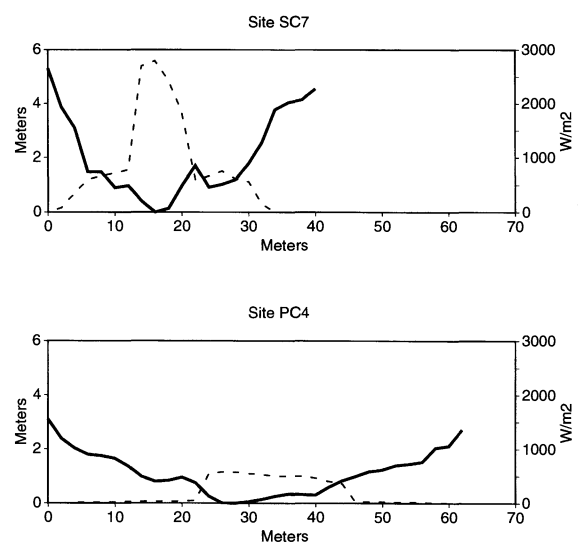
Data were collected at 37 sites in the Piru and Sespe watersheds. Sampling sites were located away from private inholdings in the National Forest and from reaches with obvious impacts of road embankments or off-road vehicle use. Sites were placed at intervals of < 5 km, with variation in spacing reflecting accessibility and the desire to sample a range of morphologic settings.

Line-intercept sampling, perpendicular to the down-valley axis, was used to record the cover of woody

species at each site (Canfield 1941). Beginning and ending points were recorded for continuous intercept lengths by individual species and for bare ground. Where foliage of multiple species overlapped, the cover of each was recorded individually. The use of the line-intercept method entailed two disadvantages: (1) species might be present at a site but omitted from the data set if they did not overlap the sampling tape; (2) the extension of tree crowns over the tape may have caused some species to be recorded beyond where they were actually rooted. The overriding advantage is that vegetation data were recorded in a form that could be exactly matched with flood data for analytical purposes: for any given segment of a cross-section, both species composition and stream power could be calculated.

Where the limits of the riparian zone were not readily apparent, sampling extended up onto the valley walls; the boundaries of the 20-yr flood zone, as subsequently estimated, defined the portion of the data used for analysis.

At each site, the valley bottom cross-section was surveyed with an automatic level, tape and rod. Measurements were taken at 2-m intervals along the tape, except where closer intervals were required to capture significant slope breaks. The tape was left in the same location for both the vegetation and cross-section surveys, so that the recorded topography (and subsequently calculated stream power) could be exactly matched with the recorded vegetation. Modal particle size of the substrate surface was visually estimated and recorded by size class (< 2 mm = sand; 2 - 64 mm = gravel; 64 - 256 mm = cobble; 256 - 4096 mm = boulder; > 4096 mm = 'bedrock').



**Fig. 2.** Examples of contrasting valley morphology. Solid lines depict topographic cross-sections; dashed lines show distribution of unit stream power. Note vertical exaggeration.

### Stream power

The estimation of stream power for this study employed a two-step process. The first step was estimation of the discharge of various recurrence interval floods at each site; the second was the use of the HEC-2 computer program (Anon. 1991) to develop the hydraulic parameters to determine for each flood recurrence interval how stream power would be distributed across the valley bottom. Fig. 3 shows a schematic portrayal of the data sources for these steps.

Discharge ( $Q$ ) for each site was estimated indirectly, with a procedure developed by the US Army Corps of Engineers (Anon. 1985) in a study of three watersheds, which included the study area. That study followed the guidelines published by the US Water Resources Council (Anon. 1982) to generate an empirical equation specific to the area, which calculates the geometric mean flood for a site as a function of drainage area, precipitation characteristics, and a coefficient that incorporates geographic variables such as soils, vegetation and geology. Index frequency curves are provided to convert the geometric mean flood to estimates of discharge for floods of varied recurrence intervals.

In the present study, estimates for the 20-yr recurrence interval flood were used. Smaller floods (i.e. with shorter recurrence intervals) would not reach all of the riparian vegetation at several sites, and substantially larger floods have such long return intervals that much of the vegetation at any given time is not likely to have experienced them. In addition, because extent of the 20-yr flood was used to define the sample area, this ensured a match between the extent of the vegetation data and hydrologic data. Regression analyses using shorter recurrence intervals – not reported here – failed to produce significantly better results, due in part to the skewing of data by the numerous zero values for the portions of the riparian zone not reached by the smaller floods.

In order to determine the distribution of stream power across each cross-section, rather than the total stream power expended at the site, the measure of unit stream power ( $\omega$ ) was used. Unit stream power is the power per unit area of the streambed (Bagnold 1966, 1977; Costa 1983; Baker & Costa 1987), and can be calculated as:

$$\omega = \gamma DS v \quad (1)$$

where  $\omega$  = unit stream power in  $\text{W/m}^2$ ;  $\gamma$  = specific weight of the fluid in  $\text{N/m}^3$  (9800  $\text{N/m}^3$  for clear water);  $D$  = depth of flow in m;  $S$  = energy slope (which is dimensionless);  $v$  = flow velocity in m/s.

For this study,  $\gamma$  was taken to be 9800  $\text{N/m}^3$ . Fluid density is actually likely to be greater during floods, but Costa (1983) noted that accurate estimation of this variable for floods is unlikely, and cited earlier research

suggesting that it makes little difference to the end result; his empirical examples demonstrated that satisfactory results could be achieved using the clear water value. The energy slope ( $S$ ) and the distribution of values for  $D$  and  $v$  across the floodplain were calculated with the HEC-2 computer program developed by the US Army Corps of Engineers' Hydrologic Engineering Center. HEC-2 calculates these variables through an iterative computational procedure that is notable for its capability of incorporating the assumption of gradually varied flow (for details, see Feldman 1981; Anon. 1991).

The HEC-2 program required as input data (1) the dimensions of the valley bottom; (2) a starting slope estimate for the first iteration; (3) discharge; and (4) Manning's roughness coefficient ( $n$ ).

The cross-section surveys recorded in the field provided the dimensional data. The initial slope estimate was taken from slope measurements on 1 : 24 000 topographic maps. This is an adequate substitute for water surface slope in the absence of surface flow during the surveys (Costa 1983; Magilligan 1988), and may indeed be more meaningful than field surveys of slope in settings with variable microtopography (Graf 1983; Bendix 1992a). The discharge was provided by the estimates described above.

Manning's  $n$  was a critical variable, as its considerable variation across the valley bottom might be expected to cause variation in  $v$ , and consequently in  $\omega$ . Values for  $n$  were selected following Arcement & Schneider (1989). Their procedure represents a significant improvement over past methods of estimating  $n$ , which relied on subjective comparison with photographs. It involves calculating separate values for each distinctive portion of the valley bottom; typically this requires calculations for the channel and for each section of floodplain in which the factors influencing roughness are moderately homogeneous. The value for the channel is calculated as

$$n = (n_b + n_1 + n_2 + n_3 + n_4) m \quad (2)$$

where:  $n_b$  = a base value of  $n$  for a straight, smooth channel in natural materials;  $n_1$  = a value for the effect of surface irregularities;  $n_2$  = a value for variations in shape and size of the channel cross-section;  $n_3$  = a value for obstructions;  $n_4$  = a value for vegetation and flow conditions;  $m$  = a correction factor for meandering of the channel.

Values for these components of  $n$  range from 0.000 (e.g.  $n_3$  in a channel with negligible obstructions) to 0.100 ( $n_4$  with dense vegetation high enough to match the depth of flow). The calculation for the floodplain segments is very similar, with the variables redefined to represent roughness elements on the floodplain. Constant values of 0.0 and 1.0 are assigned to  $n_2$  and  $m$ , because there are no floodplain equivalents for these variables.

For each equation, Arcement & Schneider (1989) provided detailed tables to guide the assignment of numerical values to the variables. In this study, the descriptions in their tables were compared to field notes and photographic slides of the cross-sections. For the determination of values for  $n_4$ , the vegetation cover data were particularly useful.

For each cross-section, then, the data input into HEC-2 included (1) the elevations every two m across the valley bottom (from the field surveys); (2) the map-derived slope measurement; (3) the estimate of discharge for the 20-yr flood at that site; and (4) the calculated values of  $n$ . For the latter, the input file specified each point in the cross-section where there was a change in roughness.

The program, in turn, generated output that included (1) the energy slope for the entire cross-section; (2) the flood stage (water surface height) for the entire cross-section; and (3) the flow velocity, including specification of the changes in velocity at different parts of the cross-section. The program supplies the last of these, velocity variation within the cross-section, by subdividing the cross-sections into segments of constant depth and roughness (hence the importance of an objective measure of  $n$ ), and calculating flow conditions in each.

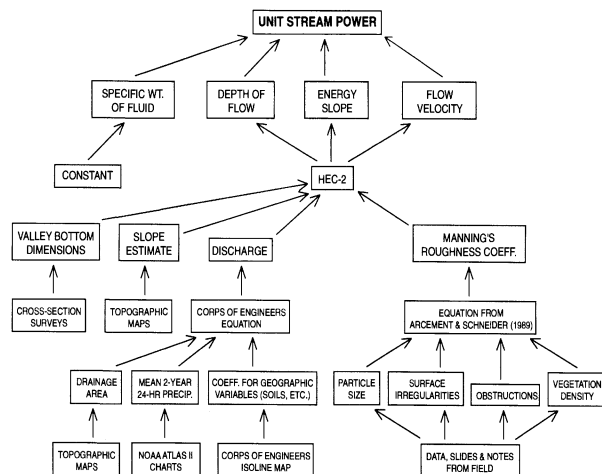
In the actual calculation of stream power, the portion of the cross-section that fell within the 20-yr flood zone (the limit of the riparian zone for purposes of analysis) was first divided into 4-m segments of horizontal distance. The 4-m length was chosen because it was short enough for comparison between segments to capture the variability of stream power across the valley bottom, yet long enough to allow the presence of multiple plant species per segment (analytical attempts

using 2-m segments yielded many with so few species that ordination of the vegetation data was precluded). There were 393 4-m segments in total from the 37 sites, each constituting one observation for analytical purposes. A value of unit stream power was then calculated for each segment by applying equation (1). For each,  $\gamma$  was given a constant value (see above).  $D$  was calculated by taking the mean height of the segment above the thalweg (the lowest point of the channel) as determined by the field surveys, and subtracting it from the flood stage in the HEC-2 output.  $S$  was the value output by HEC-2 for the entire cross-section, and  $v$  was the mean of the velocity values from HEC-2 for that segment of the cross-section. Fig. 2 provides examples of how unit stream power was distributed across two contrasting valley-bottom sites.

It should be noted that the multiple steps in the estimation of discharge, and subsequently of stream power, allow many possibilities for error to creep into the stream power estimates. However, because the procedure was applied systematically and consistently throughout, any error is likely to be consistent (i.e. over- or underestimates for all of the cross-section segments). For the purposes of establishing a relationship with vegetation, it is the relative rather than the absolute values that are critical; errors in the estimation procedure should not substantially affect the former.

#### Height above the water table

Since it was not practicable to dig down to the water table, vertical distance above the stream channel bottom was used as a surrogate for this variable. This measure has been used in past research in this region (Parikh 1989, Fig. 8); it is based on the assumption that the water table elevation is systematically related to the stream's elevation (Osterkamp & Hupp 1984). Zimmerman (1969) validated that assumption by excavation to the water table in an ecological study in Arizona. In this study, the cross-section surveys provided data to calculate the mean height (in m) above the stream thalweg for each of the 4-m segments. Although stream power may generally be expected to decrease with height, suggesting a potential for confusing the influence of these two variables, that relationship is very inconsistent (due to substantial horizontal variation of  $v$ ), hence height above the water table and stream power were not highly correlated (Pearson's  $r = -0.36$ ). Site PC4 in Fig. 2 provides an example of the inconsistent relationship between stream power and depth: unit stream power decreases much more abruptly than the topography rises, in this case due to dense thickets of *Salix lasiolepis* along the channel margins that substantially increase roughness.



**Fig. 3.** Schematic diagram of inputs for calculation of unit stream power.

### Vegetation and stream power

Cover values of woody species within the 4-m transverse segments were used in this analysis. Ordination was used to extract axis scores that could serve as composite measures of vegetative composition. The cover values for woody species were subjected to Detrended Correspondence Analysis (DCA) (Hill & Gauch 1980), using CANOCO 3.12. All species that appeared in at least four of the 395 samples were included.

Sample scores on the first axis were used as the dependent variable in regression models testing the influence of unit stream power and height above the water table. Three regression equations were calculated for the data from each of the watersheds: one with each of the independent variables, and one including both. In addition, plots were generated to show the relationship of the most common individual species to unit stream power and height above the water table. This indirect gradient analysis was chosen in preference to Canonical Correspondence Analysis (CCA) because it allowed the use of readily interpretable linear regression and the associated diagnostic tests (Aplet et al. 1998).

As noted earlier, substrate is another environmental variable which may vary within, as well as between, valley cross-sections. Analysis of variance (ANOVA) was used to test the contribution of substrate size class on the residual variance from the regressions.

The clustered spatial origin of the data raises concern about spatial autocorrelation, because segments from a given site may be so similar as to cause a violation of the assumption that the error terms in the regression equations are unrelated to each other. This possibility was tested by calculating the overall Moran MC-values for the residuals from each of the equations (Griffith 1993).

## Results

The first four axes of the DCA, incorporating 22 species, had eigenvalues of 0.926, 0.863, 0.721 and 0.617. Initial analyses showed negligible relationships between the environmental variables considered here and the second and higher axes, so the analysis reported here focuses on the first axis. Large differences amongst eigenvalues suggested that the instability which has been reported for some uses of CANOCO is not an issue with these data (Oksanen & Minchin 1997).

The relationship of individual species to axis 1 is indicated by the species scores (Table 1). The regressions of the axis scores against unit stream power and height above the water table yielded varied results (Table 2). The regressions for Sespe Creek show a modest role for stream power affecting vegetation composition.

**Table 1.** Woody species sampled within the 20-yr flood zone\*. Species that were included in analyses are ranked by their scores on the first axis of DCA ordination.

Species	Axis score
<i>Quercus berberidifolia</i>	6.52
<i>Platanus racemosa</i>	5.40
<i>Adenostoma fasciculatum</i>	5.11
<i>Eriogonum fasciculatum</i>	4.51
<i>Lepidospartum squamatum</i>	4.07
<i>Ceanothus leucodermis</i>	3.25
<i>Toxicodendron diversilobum</i>	3.14
<i>Chrysothamnus nauseosus</i>	3.11
<i>Cercocarpus betuloides</i>	3.06
<i>Artemisia tridentata</i>	2.70
<i>Quercus chrysolepis</i>	2.55
<i>Populus fremontii</i>	2.36
<i>Salix exigua</i>	2.12
<i>Pinus ponderosa</i>	1.84
<i>Eriodictyon crassifolium</i>	1.69
<i>Salix laevigata</i>	1.55
<i>Rosa californica</i>	1.05
<i>Alnus rhombifolia</i>	0.97
<i>Ephedra viridis</i>	0.87
<i>Salix lasiolepis</i>	0.61
<i>Baccharis salicifolia</i>	0.33
<i>Tamarix chinensis</i>	-0.05

\**Arctostaphylos glauca*, *Pinus monophylla*, *Quercus agrifolia*, *Rhus trilobata* and *Rubus ursinus* occurred in fewer than four samples, and were consequently omitted from statistical analyses.

Height above the water table explains less, and when stream power and height above the water table are entered together, the explanatory contribution of the latter is insignificant.

The regression results for Piru Creek are more complex. Here, unit stream power (by itself) has no predictive role, while height above the water table does have a significant impact. When both variables are used in the model, however, each makes a significant contribution, and explained variance increases substantially.

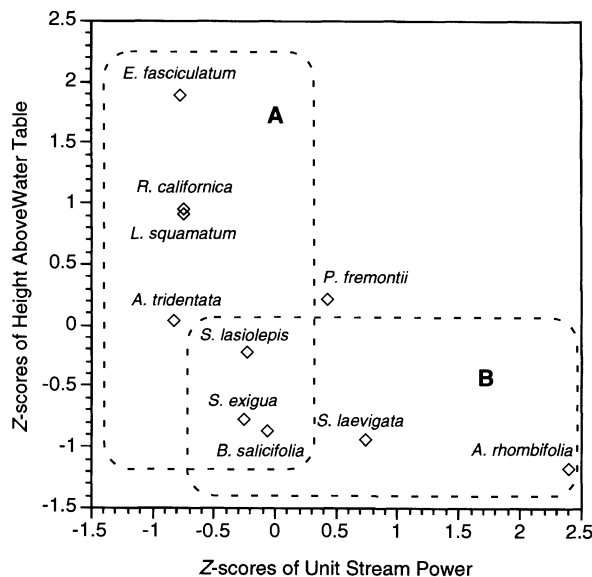
The Moran MC-values for the residuals from the regression equations ranged from 0.27 to 0.58, indicating weak to moderate spatial autocorrelation (Griffith 1993). This suggests that the results should be interpreted cautiously, as the standard errors of the estimates may be unreliable.

A plot of the distribution of the 10 most abundant species (Fig. 4) shows species in two (overlapping) groups. One group (A) is concentrated where stream power is below average; these do however separate out along the height above the water table axis. The other group (B) is found at a below average distance from the water table, but segregates on the stream power axis. Only one species, *Populus fremontii*, falls outside both groups. Fig. 5 shows the response to stream power in more detail, with boxplots showing the range of distribution of the same 10 species along the stream power gradient.

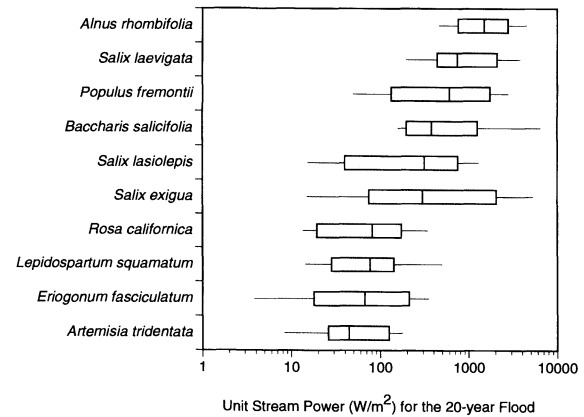
**Table 2.** Regression models testing influence of stream power and height above the water table on first axis DCA-sample scores in each watershed.

Water-shed	Predictor variable	(Standardized) Parameter value	Parameter significance
Sespe Creek	Unit Stream Power (Log) $R^2 = 0.17, n = 226, p < 0.001, MC = 0.54$	-0.414	$p < 0.001$
Sespe Creek	Height above the water table $R^2 = 0.11, n = 226, p < 0.001, MC = 0.58$	0.342	$p < 0.001$
Sespe Creek	Unit Stream Power (Log) Height above the water table $R^2 = 0.18, n = 226, p < 0.001, MC = 0.53$	-0.332 0.127	$p < 0.001$ $p > 0.05$
Piru Creek	Unit Stream Power (Log) $R^2 = 0.00, n = 167, p > 0.05, MC = 0.30$	0.018	$p < 0.05$
Piru Creek	Height above the water table $R^2 = 0.22, n = 167, p < 0.001, MC = 0.32$	0.466	$p < 0.001$
Piru Creek	Unit Stream Power (Log) Height above the water table $R^2 = 0.29, n = 167, p < 0.001, MC = 0.27$	0.318 0.619	$p < 0.001$ $p < 0.001$

ANOVAs modeling the influence of substrate particle size on the residuals from the multivariate regressions for each watershed suggest a minimal impact for this variable. In Sespe Creek, the relationship was insignificant ( $F = 0.49$ ;  $df = 225$ ;  $p > 0.05$ ). In Piru Creek, the relationship was significant ( $F = 5.70$ ;  $df = 166$ ;  $p < 0.05$ ), but the  $R^2$  was minimal (0.06).



**Fig. 4.** Relationship of the 10 most abundant species to unit stream power and height above the water table. Plotting positions reflect the median values for the segments in which that species had  $\geq 25\%$  cover. Box A encloses species plotting at less than the mean for stream power, box B encloses those plotting below the mean for height above the water table.



**Fig. 5.** Distribution of the 10 most abundant species along the unit stream power gradient. Values for each species are based on the segments in which that species had  $\geq 25\%$  cover. Center-lines mark medians, boxes enclose the 25th to 75th percentiles, and lines extend to the 10th and 90th percentiles.

## Discussion

The contrasting regression results from the Sespe and Piru watersheds emphasize that the impact of stream power (both in an absolute sense, and relative to height above the water table) is spatially quite variable. One confirms a straightforward and significant role for stream power, while the other suggests a complementary relationship between the two independent variables in which the influence of each is obscured unless they are considered together (note that the standardized parameter for height above the water table actually increases when stream power is included in the model). There are a variety of possible explanations for the differences between the relationships in the two watersheds, chiefly involving lithologic variation, but no means to definitively test them (Bendix 1992b). For example, Zimmerman (1969) found that many riparian species in Arizona do not reach the water table at all, except where shallow alluvium overlies impermeable bedrock so that the water table is held near the surface (elsewhere they are dependent on ephemeral near-surface moisture stored after rain or floods). In the present study, crystalline bedrock, the most impermeable type (Dunne & Leopold 1978) occurs only in the Piru watershed, where it is common (Bendix 1992b). It is possible that height above the water table assumes more importance along Piru Creek because this lithologic distinction makes it more likely that the water table will actually be within reach of the vegetation. Whatever the reasons, the results demonstrate that vegetation-hydrology relationships can vary significantly even within a limited geographical area.

Some of the complexity of the relationships modeled in the regression equations derives from the use of a



dependent variable (the DCA axis scores) that reflects the varied responses of multiple species. Figs. 3 and 4 illustrate the highly variable environmental affinities of the most common species sampled in the riparian zone. Of these, *Eriogonum fasciculatum*, *Rosa californica*, *Lepidospartum squamatum* and *Artemisia tridentata* are limited to the lowest stream powers. The values plotted for *E. fasciculatum* and *A. tridentata* understate this trend because both occur outside of the 20-yr flood zone that was sampled. Had the sample been extended to the surrounding slopes, they would have lower median values of stream power and higher median values of height above the water table. Neither species is well suited to withstand the impact of floodwaters, as field observations suggest both establish shallow root systems, and the stems of mature *A. tridentata* are notably brittle. Indeed, their distribution suggests all four species are apparently ill-equipped to survive high-energy floods, and thus occupy a marginal position in the riparian zone. That margin must be particularly critical for *L. squamatum*, as it is generally limited to alluvial substrates (Smith 1980; Hanes et al. 1989).

The other six are all obligate riparian species, thus it is no surprise that all have relatively limited distance to the water table, and somewhat higher stream power values. They do, however, show distinct spacing along the stream power gradient. The species found in the highest stream power locations (*A. rhombifolia*, *S. laevigata*, *P. fremontii*) are well-suited to resist floods. The presence of mature individuals of all three attested to at least several years survivorship. Field observations following floods in these and other nearby streams suggest that *S. laevigata* and *P. fremontii* may grow large enough to be relatively invulnerable to mechanical destruction (DBH frequently > 60 cm; Bendix unpubl. data), and their greater overall size ensures that relatively few individuals must survive to maturity for these species to contribute significantly to the overall cover. *Alnus* is generally smaller (although Faber et al. 1989 describe it as reaching 1 - 3.5 feet diameter, all of those seen in the study area were smaller), but its combination of solid rooting and moderate-sized but flexible stems allows it to survive severe floods relatively unscathed. It also appears to germinate in coarser substrates (i.e. cobbles and boulders) than *P. fremontii*, which would, once grown, make it less vulnerable to excavation by floods. McBride & Strahan (1984b) noted preferential flood survival of species rooted in coarse material, and similarly attributed it to the less erodible substrate. All three species sprout vigorously from stumps and downed logs, so that even when individuals are knocked down by floods the species retain a presence at the site.

The remaining three of the most common species, *S. lasiolepis*, *S. exigua* and *B. salicifolia*, constitute an

intermediate group that does not concentrate in locations of extreme stream power (Fig. 4), but which are certainly capable of growing there (Fig. 5). It is notable that these species are quite flexible (as is *S. laevigata* where it does not grow to tree size). That flexibility presumably reduces their likelihood of stem breakage by floods (McBride & Strahan 1984b), but does not confer invulnerability – it is not uncommon to find that extensive patches of *B. salicifolia*, for example, have vanished in the wake of large floods. This relative weakness may be offset by the ability to quickly re-occupy flood-cleared sites, however. Both *S. exigua* and *B. salicifolia* have been described as quick and effective pioneers of open alluvium (Holstein 1984; Hanes et al. 1989).

The interpretation of the results as they regard the influence of stream power must include recognition of the role of history. At the time that these data were collected, it was 7 yr since the calculated 20-yr discharge had last been exceeded (Ventura County Flood Control Department, unpubl. data) at site SC-7.1 on Sespe Creek, which has the best long-term stream gage records in the study area. Because the study area includes just two watersheds in an area characterized by frontal rather than convective precipitation, it is reasonable to assume that the floods recorded at SC-7.1 represent the hydrologic events at all of the sites.

Had the data been collected immediately after the 20-yr flood, we could presume that the only vegetation present in a given location was that which could actually survive the stream power that had been exerted there (and it seems likely, therefore, that the statistical relationships tested here would have been stronger). With the passage of time, however, the composition of the vegetation may altered by successional processes (Johnson et al. 1976; McBride & Strahan 1984a; Hupp 1992; Baker & Walford 1995). Or, if smaller, more frequent floods are sufficient to at least partially disrupt succession, vegetation change may be more limited, in an oscillatory equilibrium with the hydrologic regime. Either way, we must recognize that the composition of the riparian vegetation is non-static both before and after large floods occur. At any given point a flood may restart, redirect, or fail to influence the development of the vegetation. The observed vegetation will therefore be different depending not only on stream power but also on the composition and condition of the vegetation when the flood occurred and the length of time since its occurrence.

Such historical factors may help to explain the limited  $R^2$ -values for the regressions reported here. An additional reason is the limitation of the independent variables to unit stream power and height above the water table. Because the objective of this study focused on the spatially detailed impacts of floods, the analysis

was limited to the factors that vary at the finest measurable (i.e. within-site) scale. Substrate, the only other transverse-scale variable, proved to be of minimal importance. Previous analyses have combined and compared the impacts of these variables with those, like elevation, aspect and fire history, that operate at coarser scales (Bendix 1994b). The large unexplained variance in both that analysis and the present one may support, at least for dynamic environments, Vale's (1989) contention that environmental conditions set the possible limits within which historical events influence actual vegetation patterns.

The influence of environmental conditions, however, is the least contingent and most readily quantifiable determinant of vegetation. At any given point, the vegetation will represent the combined influence of the environmental factors that act at different scales, necessitating a clear understanding of each. For example, *Salix lasiolepis* tends to be found at somewhat higher elevation sites in the study area than *Baccharis salicifolia* (Bendix 1994a). Consequently, despite their similar positioning relative to stream power and height above water table (Fig. 4), they are not necessarily found together, but instead occupy similar within-site positions at different places in the watershed. Their distribution, then, cannot be understood without recognizing the influences felt at both scales.

Because distance from the channel seems such an intuitively important variable, vegetation patterns at this transverse scale have long intrigued ecologists (Illichevsky 1933; Malanson 1993). At the transverse scale, the results of this study confirm that we can enhance our understanding of flood impacts on riparian vegetation by using methods and concepts from fluvial geomorphology that allow quantitative estimates of the actual energy exerted by floods. The fact that the role and importance of flooding varies from one watershed to (literally) the next, as well as between species, suggests that such procedures are of value; we cannot assume that simple measures like distance from the stream channel actually reflect a flood response.

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