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FACTORS CONTROLLING STRUCTURAL AND FLORISTIC VARIATION OF RIPARIAN ZONES IN A MOUNTAINOUS LANDSCAPE OF THE WESTERN UNITED STATES

A.G. Merrill¹, T.L. Benning², and J.A. Fites¹

ABSTRACT.—We examined landscape patterns in the physical conditions and vegetative composition of montane riparian zones to identify their most important sources of variation. Information on plant species cover and on physical characteristics that occur at coarse, medium, and fine scales was collected for 144 riparian plots located throughout the Lake Tahoe Basin, which straddles the California-Nevada border in the western United States. Constrained and unconstrained ordination analyses were used to identify the most important correlates of physical form and plant species composition. Through multivariate analysis of environmental variables (principal components analysis), vegetation data (detrended correspondence analysis), and the combined relationship between the environmental and vegetation data (canonical correspondence analysis), we consistently found that the greatest variation occurred along a gradient of decreasing valley width, decreasing stream sinuosity, and increasing stream slope. Although surface characteristics reflected a 2nd important source of variation in physical conditions, plant species distribution was not strongly correlated with riparian surface conditions. Strong correlations among physical variables that occur at different scales, such as between valley form and geofluvial surface and between geofluvial surface and surface conditions, support the use of a physically based hierarchical framework for organizing riparian zones within the landscape. Such a hierarchical framework would be useful for interpreting patterns in riparian structure and process at different scales and could be applied to riparian zones in other mountain landscapes of the western United States and elsewhere. Moreover, our finding that riparian plant species composition is most strongly correlated with environmental variables that occur at coarse to moderate scales, most of which can be derived from existing data, supports the idea that modeling montane riparian community distribution using topographic and remotely sensed data could be useful; however, a large degree of species variation, unexplained by the variables we collected, indicates that other variables, perhaps disturbance regime, should be included in such a venture.

Key words: riparian, ordination, Lake Tahoe Basin, hierarchy theory, montane vegetation, landscape ecology, variation.

Nomenclature: Hickman (1993).

It has long been recognized that riparian zones perform important services, including improvement of surface and groundwater quality, provision of high quality habitat, reduction of flood risk and erosion, and increased stabilization of banks. Growing appreciation of the importance of riparian zones and other wetlands has resulted in dramatically increased expenditures for protection and restoration of these systems. For example, The CALFED Bay-Delta Program (CALFED Bay-Delta Program 1999) has approved approximately \$254 million for wetland and watershed restoration projects within the California Bay Delta watershed. In 2003 the Lake Tahoe Restoration Act was signed into law; this act authorized federal expenditures of up to \$300 million to fund a 10-year, \$908-million Environmental Improvement Pro-

gram at Lake Tahoe, which includes extensive watershed restoration projects. In spite of this public attention and expenditure, a watershed-to-landscape-scale understanding of the factors driving variation in the composition and dynamics of riparian ecosystems is lacking. Understanding how riparian systems differ structurally and functionally in the landscape and what factors control this variation would improve our ability to predict effects of human activities on services that riparian ecosystems provide.

We use hierarchy theory to organize observed variation in the physical and vegetative characteristics of riparian zones in a mountain landscape. Hierarchy theory postulates that landscapes are composed of entities organized as nested units (O'Neill et al. 1986, 1989). The

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behavior of units at one given level of the hierarchy is controlled by environmental constraints imposed by units at a scale above and by the biotic potential of the system's components at a scale below (O'Neill et al. 1989). Hierarchy theory has been applied to explain the distribution of terrestrial ecosystem types (Albert et al. 1986) and to develop models that predict variation in ecosystem function and processes, including response to disturbance and biogeochemical cycling (Zak et al. 1986, Host et al. 1987, Wu and Loucks 1995, Palik et al. 2000, Sauchyn 2001).

Although the concept of hierarchy theory might be generally applicable, the elements within a hierarchy likely vary among landscapes. Different types of landscapes have characteristic sets of physical features that control variation in their associated riparian zones (Malanson 1993). For example, the valley of the lower Mississippi has very low topographic relief and abundant water. In this landscape floristic variation tracks subtle shifts in topography that alter the extent and duration of flooding and the chemistry of sites within the riparian zone (Trettin et al. 1994). Less subtle shifts in landscape characteristics control the riparian environment in mountainous regions. In the mountains, differences in coarse-scale variables such as orographic weather patterns, parent material type, and effects of glaciation can occur within a landscape and within a 1000-km² watershed.

These coarse-scale factors constrain several finer scale factors related to the montane riparian environment. For example, climate, geology, and glacial and tectonic histories of a surrounding watershed shape the valley width and gradient (Mount 1995, Tabacchi et al. 1998). Therefore, valley shape should be highly correlated to these coarse-scale variables. Geofluvial surfaces formed within the valley floor are dependent, in part, on the coarser scale variable of valley shape (Tabacchi et al. 1998). For example, slumping and scouring floods that occur in narrow, steep valleys leave behind denuded banks and narrow, ephemeral floodplains. In contrast, meanders in a wide valley floor dissipate the stream's energy laterally, resulting in a complex transverse profile of wide floodplains, point bars, and terraces. These observations led us to expect certain valley shapes to be correlated with frequency of particular sets of geofluvial surfaces.

The geofluvial surface itself is a product of local hydrologic flows and sediment transport. Particle size in riparian alluvial soils can be affected by the energy of water flow that deposited the sediment; similarly, flood frequency and intensity can affect riparian soil particle size. Soils in riparian areas subject to frequent scouring or depositional disturbance are young and have little to no structure. Riparian soils in broad, depositional valleys will vary in relation to the history of the meander pattern of the river (Hawk and Zobel 1974). Thus, the well-developed riparian soils are likely to be those in the retired terraces of wide, alluvial valleys. In addition, the elevation above stream level at which these surfaces form limits the type and amount of subsequent deposition and removal. Thus, the geofluvial surface influences and is expected to be correlated with soil texture and development (Knighton 1984, Osterkamp and Hupp 1984). These relationships among coarse-scale (e.g., parent material, climate, and geomorphic regime) and finer scale characteristics (e.g., soil characteristics, geofluvial surface, channel form, and local hydrology) are generally accepted in the current riparian literature as the primary controls over riparian structure (Malanson 1993, Tabacchi et al. 1998). We collected data on these variables and tested for correlations among them to see if such a hierarchy of control over riparian structure and composition could be demonstrated in a mountain landscape. Specifically, we hypothesized that, in the mountain landscape of the Lake Tahoe Basin, factors that occur at coarse (10-km²), stream-reach (100-m²), and site (1-m²) scales correlate to riparian structure and species composition.

We also expected to find that the distribution of riparian plant species is correlated to the same set of variables that define the greatest degree of physical variation among riparian zones. Other researchers have demonstrated strong correlations between abiotic and biotic components of riparian systems (Wistendahl 1958, Sigafos 1961, Hawk and Zobel 1974, Hupp and Osterkamp 1985, Harris 1988). Hupp and Osterkamp (1985) reported a significant correlation between geofluvial surface and specific riparian vegetation for riparian habitats in the southeastern United States. The authors attribute this correlation to species-specific flood tolerances, differences in geofluvial surface flood frequency, and flood duration (see

also Auble et al. 1994). Hupp (1992) later added to this interpretation by linking stream-reach-scale processes of erosion and deposition to riparian plant community composition. Thus, studies from the southeastern United States highlighted the importance of geofluvial surfaces and attendant variations in soil texture and hydrology in affecting plant community composition. In California, Stromberg and Patten (1990) focused on the effects of stream flow on riparian vegetation in the Sierra Nevada. This work indicated that correlations between changes in stream flow and shifts in plant composition are due to differential seedling growth and survival in response to variation in substrates. In the eastern Sierra Nevada, Harris (1988) found that riparian vegetation along 10 mountain streams was significantly correlated to geomorphic forms when nested within a broader pattern of valley type. Friedman et al. (1996) reported that flood history and post-flood succession are the most important factors influencing the distribution of riparian plant species. Thus, previous studies in the American West point to the importance of valley form, geofluvial surface, and hydrologic processes as correlates to the distribution of riparian plant species.

Our objectives were to (1) identify factors that explain the greatest variation in the physical structure of riparian zones in a mountain landscape, (2) characterize variation in riparian plant species composition, (3) identify physical factors that correlate to the greatest variation in floristic composition, and (4) describe a hierarchical framework that accounts for riparian zone structure and floristic composition. For this project, we defined the riparian zone broadly to include the retired terraces as well as gravel bars along the valley bottom. However, we only included seasonally or less frequently flooded wetlands and terraces associated with lotic systems; permanently flooded wetlands were not included. We conducted this research in the mountainous landscape of the Lake Tahoe Basin (LTB) in the western United States because LTB provides a wide range of variation in coarse- as well as fine-scale variables within a distinct and relatively compact area. Issues related to watershed and wetland restoration are also extremely important in LTB, and this research was performed in hopes of providing needed baseline data for restoration and conservation projects in the area.

METHODS

Study Area

Lake Tahoe is an alpine ultra-oligotrophic lake with 63 tributaries; its watershed encompasses 2 distinct climatic zones. Located at the crest of the Sierra Nevada (39°N, 120°W), the 800-km² watershed straddles the California-Nevada border and ranges from 1898 m to 3050 m above mean sea level. The mountain climate has short, dry summers and long, cold winters during which most (>70%) of the annual precipitation falls. The western slopes of the LTB receive relatively large amounts of precipitation, ranging from 75 cm · yr⁻¹ to 200 cm · yr⁻¹, compared to the eastern slopes, which receive an average of 40 cm · yr⁻¹. Summer (May–September) temperatures at lake level average 29.4°C, while winter (October–April) temperatures average 17.6°C (NCDC 2000). Lake Tahoe Basin includes 4 major types of bedrock geology: granite, volcanic rock, glaciated till and alluvium, and lake deposits (Fig. 1; Bailey 1974). The LTB covers 4 major vegetation zones including montane, upper montane, subalpine, and alpine vegetation (USDA Forest Service 1991). In this study we included only riparian areas within the montane and upper montane zones. We sampled the least disturbed riparian wetlands (as defined below) to provide information on intact ecosystem structure and composition.

Sampling Design and Field Procedures

We collected data on 27 environmental variables that occur at coarse (10-km²), stream-reach (100-m²), and plot (1-m²) scales; and we recorded percent cover for 203 plant species (Table 1) associated with 144 riparian plots (50 m²) in 21 subwatersheds in LTB. These plots are well distributed among physiographic regions (Table 2, Fig. 1). To include a range of coarse-scale environmental variables hypothesized to affect riparian zone structure, we divided the LTB into 15 physiographic regions based on differences in climate, parent material, extent of glaciation, and, as an additional proxy for climate, upland vegetation zone (Table 2). We merged geographic information system (GIS) layers containing information on climate, parent material, geomorphic history, and upland vegetation to create a 10-composite-layer, 1:24,000-scale map with over 200 stream-intersecting polygons

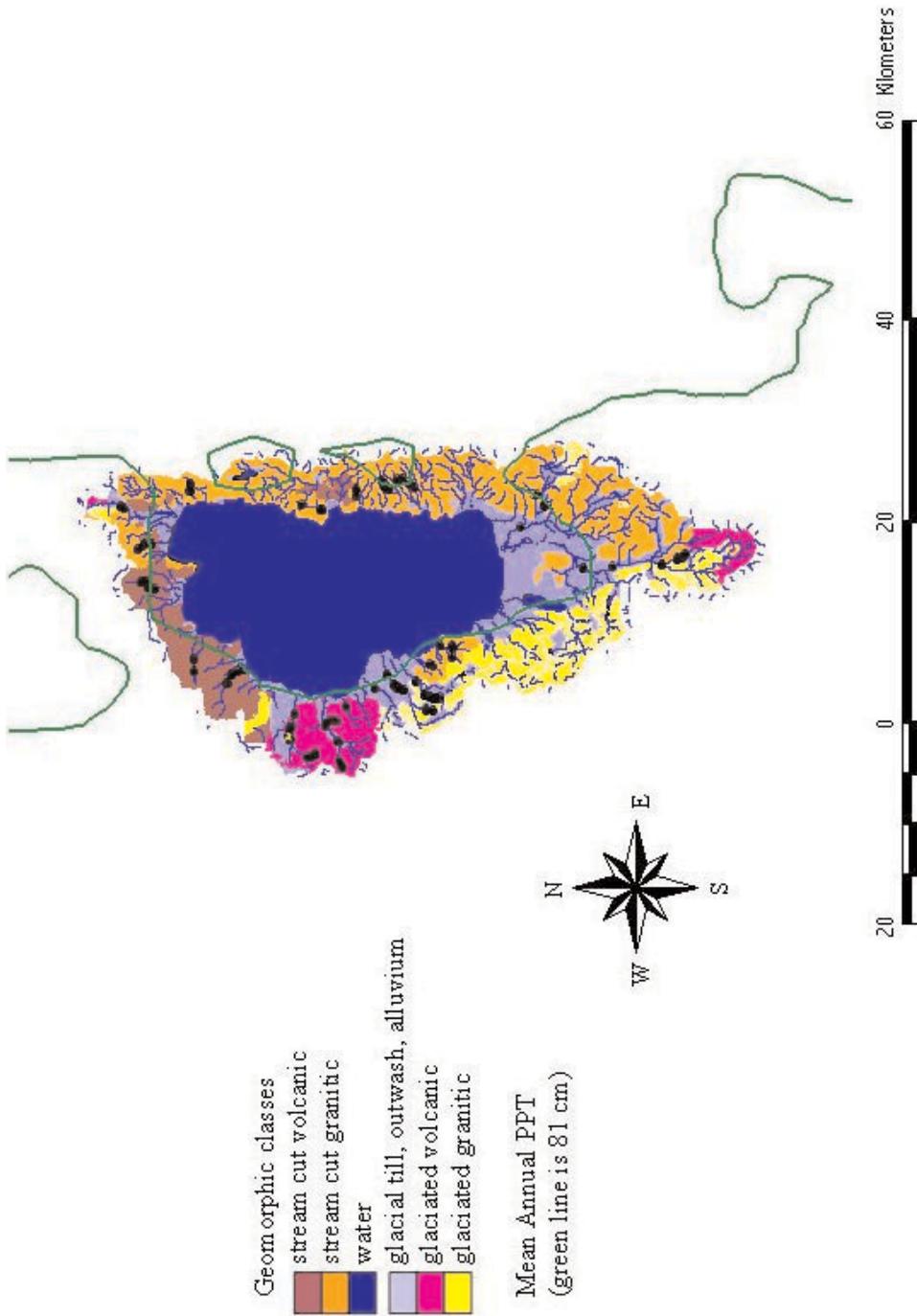


Fig. 1. Lake Tahoe Basin is located in western California and eastern Nevada. Different types of parent material and glaciation history along with areas of high and low precipitation (west and east of the 81-cm line) located within the LTB make it possible to study the effects of coarse scale environmental variables on riparian structure and plant species composition. We sampled 144 riparian research plots throughout the LTB during field seasons in 1995 and 1996.

TABLE 1. Data on abiotic and biotic characteristics collected at 3 scales.

Spatial scale	Variables
Coarse (10 km ²)	Parent material Mean annual precipitation Upland vegetation zone Flow direction Glaciation history
Reach (100 m ²)	Valley width Valley shape Channel sinuosity Valley gradient Elevation Channel bottom material Bank-full width Bank-full depth Flood-prone width
Plot (1 m ²)	Fluvial surface Distance to channel edge Community width Slope of plot Aspect of plot Average plot elevation above bank-full Rock/gravel cover Cobble/boulder cover Bare ground cover Litter cover Litter thickness Surface soil texture (upper 10 cm) Surface soil organic matter content
Plot Vegetative Characteristics	Percent cover in upper and lower canopies Total cover by plant functional group Percent cover of each species present

that averaged 33 ha in area. These polygons were numbered and categorized according to their physiographic region. Working with USDA Forest Service employees, we identified accessible areas that had not been subjected to major disturbances (e.g., fire or logging) in the past 50 years. At the end of this process we had a minimum of 10 polygons for each physiographic type for a total of 187 polygons. We visited each of these polygons over 2 field seasons but had to omit many polygons from our sample pool due to disturbance (e.g., fire, development, etc.). Within 84 polygons, we selected stream reaches suitable for sampling based on 3 criteria: (1) no obvious evidence of recent human disturbance, (2) riparian vegetation representative of the reach or adjacent reaches, and (3) >15 m horizontal distance from a road and >300 m below any road crossing. Each plot was 50 m²; plot shape varied to accommodate the irregular

shapes of the fluvial surfaces. At each site data was collected for the abiotic and biotic characteristics listed in Table 1. Our field procedures were adapted from those of Region 4 and Region 5 of the USDA Forest Service (Allen 1987, Weixelman et al. 1996).

Each plot position and elevation was recorded on 1:24,000 topographic maps by triangulating compass sitings and landforms observed on aerial photographs. At each plot we checked the accuracy of geomorphic zone assignments (Bailey 1974) by examining rock outcrops at or near the site. Similarly, we field-checked the upland vegetation zone assignment by examining species composition of the surrounding uplands. In addition, we paced the width of each valley and recorded whether the valley was V-shaped (constrained) or flat-bottomed (unconstrained). Slope, aspect, stream flow direction, and gradient were measured using a compass and clinometer. For each plot we recorded the texture of the top 10 cm of soil using the ball and ribbon technique (Brady 1984) and recorded whether soil had high, medium, or low organic content according to the extent of dark-staining material found in the samples. We made visual estimates of absolute litter cover to the nearest 1% when there was <10% cover and to the nearest 5% when litter cover was >10%. Mean litter depth was calculated from 4 randomly placed measurements per plot. Similarly, we made visual estimates of the absolute percent cover of sand, gravel, cobbles, and boulders within each plot and along the stream bottom at each associated 20-m stream reach. The geofluvial surface of each plot was categorized as 1 of the following: terrace, bank, or floodplain. Terraces were the inactive floodplain (Schumm 1977), whereas floodplains were areas within the active channel and included the "active floodplain" (Schumm 1977) and gravel and cobble bars that lay within the bank-full channel (Williams 1978).

Regardless of current water levels, we defined channel extent according to its bank-full or 2.7-year flood level (Williams 1978). We measured channel depth and width at 4 cross sections along the associated reach and recorded the mean values. We also measured flood-prone width, defined as the width of the stream channel with water levels at twice bank-full. We used the average of the vertical and horizontal distance of 4 points to the stream edge (bank-full channel) as measures of distance to channel

TABLE 2. Distribution of 144 riparian plots according to physiographic variables.

Geomorphology	Montane		Upper Montane		Totals
	Wet ^a	Dry ^b	Wet	Dry	
Alluvium	8	6	—	—	14
Lake deposits	12	—	—	—	12
Glacial till	13	4	16	—	33
Glaciated granitics	—	—	16	—	16
Streamcut granitics	4	9	4	13	30
Glaciated volcanics	—	—	19	—	19
Streamcut volcanics	10	5	—	5	20
TOTALS	47	24	55	18	144

^a“Wet” includes most of the south- and half of the north-shore watersheds as well as watershed on the western shore of Lake Tahoe where mean annual precipitation (MAP) exceeds 81 cm.

^b“Dry” includes most of the eastern shore of the LTB where MAP is <81 cm.

edge and elevation above bank-full. Community width was defined as the width of area supporting consistent plant species composition perpendicular to the stream. Stream sinuosity was calculated as the quotient of stream length over valley length (Mount 1995) as measured on 15-minute topographic maps. We visually estimated absolute cover for all live vascular plant species to the nearest 1% for species with <10% cover and to the nearest 5% for species with >10% total cover. We obtained mean annual precipitation data from the Oregon Climate Service and PRISM Services (1997a, 1997b).

Statistical Analysis

We used principal component analysis (PCA) to identify those environmental variables responsible for the greatest amount of variation in the physical characteristics of the 144 riparian plots. Detrended correspondence analysis (DCA) was used to identify major patterns in plant composition within LTB riparian zones. To simplify interpretation we organized the vegetation into indicator species groups, composed of commonly co-occurring plant species. Two-Way-Indicator-Species-Analysis (TWINSpan)—a polythetic, divisive clustering technique—was used to identify these groups (Hill 1979). Through stepwise multiple regression we identified those environmental variables that explained the greatest variation in plant species distribution summarized in DCA axes 1 and 2. Canonical Correspondence Analysis (CCA) constrains ordination of plant species data through linear regression of environmental variables. CCA was employed to further assess the relationship between environmental variables and plant species distribution (Palmer 1993). CCA

was also used as a method, 2nd to DCA, for identifying environmental variables that were most highly correlated to the distribution of riparian plant species. By comparing the DCA and CCA matrices, we could identify variation occurring in the species matrix that is not well explained by the environmental variables measured. Thus, we applied all 3 ordination techniques to (1) identify the greatest sources of physical variation and thereby define the important components in the proposed physical hierarchy (PCA); (2) identify variation in plant species composition independent of physical variables measured to illustrate the degree of plant variation captured by measured variables (DCA); and (3) quantify correlations between plant species composition and the physical variables measured to assess the link between vegetation and the physical variables included in the proposed hierarchy (CCA).

We used Monte Carlo permutation tests (Jongman et al. 1995) to test for significance of the first 3 CCA axes and the species-environment scores. To test for the species-environment relationship, plot numbers associated with the environment variables were randomized prior to ordination. The species-environment correlations and axes eigenvalues were then calculated based on this semi-randomized set. The process was repeated 100 times to estimate the likelihood of obtaining the same axis eigenvalues and species-environment scores calculated from the original nonrandomized data. Manly (1992) provides further discussion of these procedures.

To identify environmental variables that explain the greatest amount of variation in the species-environment relationship, we used a

semiautomated procedure in the CANOCO software (ter Braak 1988) called "forward selection." Forward selection is similar to stepwise regression in that a series of canonical correspondence analyses are performed as environmental variables are added one at a time. The user selects the 1st variable and then adds variables to subsequent analyses based on the increase in goodness of fit of the multiple regression. Since the input order of the environmental variables can affect the increase in goodness of fit, we altered the input sequence 10 times to ensure that we identified a consistent set of the most strongly correlated variables. See Draper and Smith (1981) for further discussion of forward selection. Additionally, as a 1st step in exploring the efficacy of developing a GIS-based model to predict the distribution of riparian plant communities, we wanted to assess the strength of the relationship between site species composition and environmental variables that could be gathered remotely. Using the Monte Carlo CCA permutation procedure, we estimated the strength of the correlation between plant species composition and variables that were or easily could be remotely acquired (i.e., parent material, glacial history, elevation, valley width and shape, and stream flow direction and gradient).

Hierarchically, landscape elements are constrained by environmental factors that occur at coarser spatial scales (O'Neill et al. 1986). If this is the case, then landscape elements should be correlated to factors that constrain them. Environmental variables were grouped into those that vary at coarse (10-km²), stream-reach (100-m²), and plot (1-m²) scales (Table 1). We tested for significant correlations between variables across and within scales using the coefficient of determination (r^2). To eliminate spurious correlations due to "data snooping" (Neter et al. 1985), the significance of each correlation was determined using the stringent Bonferroni pairwise testing procedure ($P \leq 0.10$; Neter et al. 1985). Several variables, including channel width and stream gradient, were log-transformed to meet assumptions of normality. Environmental variables were then standardized so that they shared equal means and unit variance prior to subsequent statistical analyses. One from any pair of variables with a Pearson's correlation coefficient of ≥ 0.75 was removed from the database to minimize the

effects of multicollinearity. Three variables met this condition: bank-full depth and width were highly correlated as well as flood-prone width and bank-full width. As a result, bank-full depth and flood-prone width were excluded from further analyses.

Prior to analysis, we lumped into 1 group several sedge species that were difficult to distinguish in the field and that favored similar site conditions; this group included *Carex heteroneura*, *C. lenticularis* var. *lipocarpa*, *C. abrupta*, *C. bolanderi*, *C. fracta*, *C. nervina*, and *C. nebraskensis*. Similarly, we lumped several co-occurring willow species, including Eastwood (*Salix eastwoodiae*), grayleaf (*S. orestra*), Jepson's (*S. jepsonii*), Geyer's (*S. geyeriana*), and narrow-leaf (*S. exigua*) willows with the most common shrub species of the group, Lemon's willow (*S. lemmonii*). Other willows that favor different site conditions, such as Scouler's willow (*S. scouleriana*) and shining willow (*S. lucida*), were kept separate.

In the dynamic riparian landscape, the occurrence of long-lived upland overstory tree species can reflect past site conditions that differ dramatically from current ones (Carleton et al. 1985, La Roi et al. 1988). Therefore, long-lived upland tree species were excluded from correspondence analyses. We accepted the default settings in TWINSpan, including pseudo-species cut levels. We accepted splits in the 2-way output tables where eigenvalues were >0.200 . Stochasticity in clustering of plots through TWINSpan analysis has been related to effects of infrequently occurring species (Tausch et al. 1995). To avoid this problem, species occurring in fewer than 3 sites were excluded from TWINSpan analysis. We used the following software packages to perform these statistical analyses: S-PLUS 4.5 (Insightful Corporation 2001), TWINSpan (Hill 1979), CANOCO (ter Braak 1988), and PC-ORD 4.17 (McCune and Mefford 1999).

RESULTS

Variation in Structure of Riparian Zone

We used PCA to identify those environmental variables that explained the greatest degree of variation in physical characteristics of the riparian sites. The 2 first axes explain $>30\%$ of the variability among 144 riparian plots (Fig. 2). A combination of coarse- and reach-scale

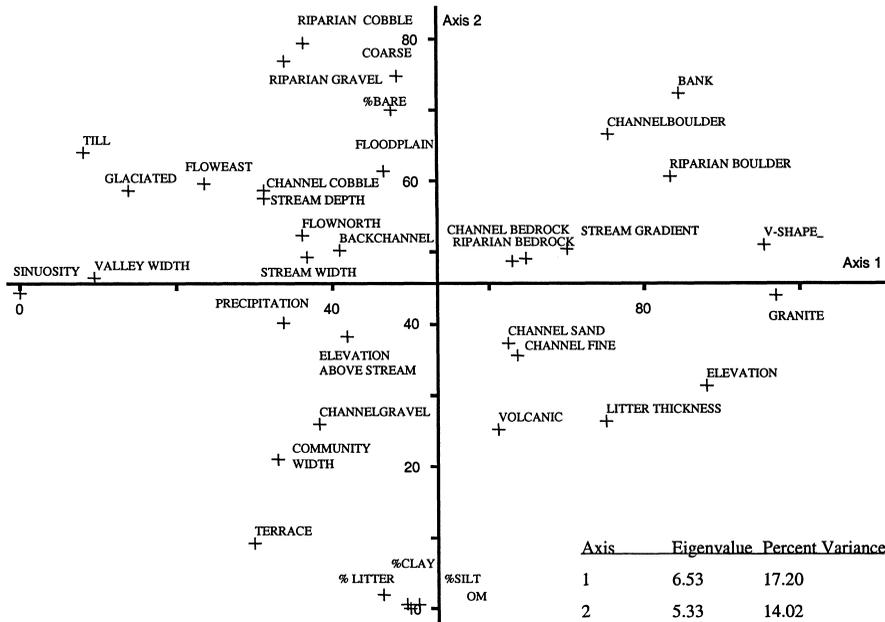


Fig. 2. Principle components analysis of environmental variables. The first 2 axes explain over 30% of the variation in physical structure of LTB riparian zones. The codes used are defined as follows: %Bare = percent bare ground; %Clay = percent clay in surface soil; %Litter = percent litter cover; %OM = percent organic matter in surface soil; %Silt = percent silt in surface soil; Backchannel = geofluvial surface is a back channel; Bank = geofluvial surface is a stream bank; Channel bedrock = percent of channel in reach that is bedrock; Channel boulder = percent of channel in reach that is boulder; Channel cobble = percent of channel in reach that is cobble; Channel fine = percent of channel that is finer than sand; Channel gravel = percent of channel that is gravel; Channel sand = percent of channel that is sand; Coarse = percent of coarse material in soil (>1 inch); Community width = width of riparian plant community; Elevation = elevation of site above mean sea level; Elevation above stream = number of cm site is above bank full; Floodplain = geofluvial surface is a floodplain; Floweast = direction of streamflow (bearing broken into “eastness” and “northness”; see methods); Flownorth = direction of streamflow; Glaciated = stream reach is in glaciated valley; Granite = parent material is granitic; Litter thickness = thickness of litter in site; Precipitation = average annual precipitation; Riparian bedrock = percent of riparian plot that is bedrock; Riparian boulder = percent of riparian plot that is boulder; Riparian cobble = percent of riparian plot that is cobble; Riparian gravel = percent of riparian plot that is gravel; Sinuosity = sinuosity of stream reach; Stream depth = average depth of stream channel at bank-full; Stream gradient = average gradient of reach; Stream width = average stream width at bank-full; Terrace = geofluvial surface is a terrace; Till = parent material is glacial till; Valley width = width of valley associated with stream reach and riparian plot; Volcanic = parent material is volcanic; V-shape = valley shape is V-shaped (as opposed to flat-bottomed).

variables were most highly correlated with axis 1, which captured 17.2% of the overall variation in site data. Axis 1 defined a gradient of decreasing valley width and stream sinuosity and increasing stream gradient (Fig. 2). Plot-scale variables associated with surface conditions were more closely correlated to axis 2 (14.0% of variance). This 2nd axis ordinated plots along a gradient of coarse, rocky surfaces associated with banks and floodplains to rich, loamy surface soil conditions associated with terraces.

To develop an hierarchical framework that could account for the variation observed, we examined correlations among physical variables

across scales. We will discuss correlations among physical variables (Table 3) based on the scale groupings (coarse, 10 km²; reach, 100 m²; and site, 1 m²). In the LTB we found that many characteristics that vary at the reach scale were strongly correlated to parent material and glaciation history, both of which varied at the coarse scale (Table 3). For example, stream reaches in glacial till, outwash, and lake deposits tended to occur in wider valleys than reaches in other parent material types. Similarly, stream sinuosity and channel width, factors that vary at the reach scale, were positively correlated to glacial till (Table 3). To some extent these correlations can be attributed to the occurrence

of glacial till and outwash at lower elevations where the depositional portions of the tributary streams occur. However, controlling for differences in precipitation (e.g., climate) and elevation, stream valleys in glacial till were significantly wider ($\text{adj-R}^2 = 0.31$, $n = 144$, $P < 0.001$) and of shallower grade ($\text{adj-R}^2 = 0.14$, $n = 144$, $P < 0.001$) than valleys in nontill parent material. Therefore, part of the correlations between glacial till, sinuosity, stream width, and valley width may be due to the direct effects of glacial till on valley form and sinuosity. In contrast to glacial till, granitic and volcanic parent materials were similarly distributed in the upper and lower portions of the watersheds of LTB. Differences in valley form of areas with granitic versus volcanic parent material were significant (Table 3). Analysis of covariance (ANCOVA) of the 52 sites that occur in stream-cut (versus glaciated) valleys, in which granitic and volcanic parent material were compared with precipitation (as a measure of climate) as a covariate, showed that stream-cut granitic valleys tend to be steeper than stream-cut volcanics ($\text{adj-R}^2 = 0.25$, $n = 52$, $P = 0.0004$). Analysis of variance (ANOVA) of these 52 sites showed that granitic valleys tend to be narrower ($\text{adj-R}^2 = 0.12$, $n = 52$, $P = 0.008$) and are more often V-shaped ($\text{adj-R}^2 = 0.31$, $n = 52$, $P < 0.001$) than are stream-cut volcanic valleys. Among glaciated areas on the western shore, stream reaches in granitic parent material were less sinuous than ones in glaciated volcanics ($\text{adj-R}^2 = 0.25$, $n = 83$, $P < 0.001$).

A few significant correlations were also found between parent material (a coarse-scale variable) and surface soil characteristics (plot-scale variables). For example, riparian areas in granite tend to have higher boulder cover than areas in volcanic parent material (Rank sums nonparametric group comparisons followed by post hoc Nemeny's test, $n = 144$, $P < 0.0001$). Soil silt and clay content were significantly higher in areas of volcanic parent material than in areas on granitic or till parent material (1-way ANOVAs followed by post hoc Tukey's HSD test, $n = 144$, $P < 0.01$). We found no significant differences in the frequency of geofluvial surfaces among types of parent material (using a contingency table and chi-square test).

Most plot- and reach-scale variables were not correlated; however, we did find that geofluvial surface was correlated to valley shape

and width, as well as to channel sinuosity (Table 3). The frequency of banks without associated terrace increases with increasing stream gradient, and terraces are more common among higher sinuosity and lower gradient reaches in flat-bottomed valleys. In addition we found that the amount of riparian area covered by boulders increased with increasing valley gradient and decreased with decreasing elevation and increasing valley width (Table 3). Other expected correlations were found among plot-scale variables, particularly variables related to geofluvial surface and surface soil characteristics. Boulders are more frequent on banks than in terraces or floodplains, whereas gravel is a more common surface material in floodplains than in terraces or banks. Terraces were correlated with more fertile soils: organic matter content, percent silt and clay in soil, and litter cover were higher in terraces than in soils of other geofluvial surfaces.

Variation in Riparian Zone Vegetation

We used TWINSpan to delineate 5 groups of frequently co-occurring species (Table 4). Groups were named by the genera of the group's most characteristic species. Detrended correspondence analysis (DCA) was used to confirm the distinctness of these species groups (Fig. 3). Both DCA axis lengths were >4 standard deviations (Table 5); therefore, sites on either end of both axes had few to no species in common (Jongman et al. 1995). The 5 remaining groups occupy unique and distinct regions of the DCA ordination space. Axis 1 most clearly separates groups 1 and 5. The plant community with the most negative axis 1 scores was represented by the *Ribes-Rubus* group (group 1) and was dominated by shrubs and the small understory tree Scouler's willow. On the other end of this axis was the *Sidalcea-Hordeum* group (group 5), which represents a community dominated by grasses and herbs. The *Salix-Carex* group (group 4), dominated by sedges, willow, and a few herbs, was most clearly distinguished from the rest with negative axis 2 scores. Grasses and herbs that prefer mesic to dry-mesic conditions had more positive axis 2 scores (Fig. 3). Species in the *Veratrum-Poa* group (group 3) were common in sparsely to moderately forested meadows adjacent to the unforested meadows of the

TABLE 3. Correlation table of environmental variables for 144 riparian plots. Pearson correlation coefficients are shown with significance determined using a Bonferonni test. Boldface type indicates $P < 0.10$.

Variable	BROAD SCALE	TILL	GRANITE	VOLCANIC	PPT	FLOW DIRECTION	GLACIATED	REACH SCALE	VAL-WIDTH	V-SHAPE VAL	VAL GRADIENT	ELEVATION	SINUOSITY	CHAN WIDTH
BROAD SCALE														
TILL	1.00													
GRANITE	-0.56	1.00												
VOLCANIC	-0.42	-0.41	1.00											
PPT	0.08	-0.23	0.25	1.00										
FLOW DIRECTION	0.34	-0.32	-0.04	0.35	1.00									
GLACIATED	0.57	-0.48	-0.16	0.62	0.40	1.00								
REACH SCALE							1.00							
VALWIDTH	0.56	-0.43	-0.19	0.12	0.16	0.38		1.00						
V-SHAPE VAL	-0.24	0.44	-0.14	-0.23	-0.28	-0.29		-0.55	1.00					
VAL GRADIENT	-0.31	0.25	0.13	0.04	-0.11	-0.17		-0.41	0.41	1.00				
ELEVATION	-0.44	0.33	0.28	0.09	-0.45	0.27		-0.22	0.31	0.37	1.00			
SINUOSITY	0.51	-0.43	-0.18	0.12	0.35	0.34		0.54	-0.54	-0.69	-0.39	1.00		
CHAN WIDTH	0.54	-0.37	-0.29	0.21	0.26	-0.41		0.33	-0.39	-0.34	-0.49	0.47	1.00	
CHAN BOULDER	0.00	0.11	-0.04	0.13	-0.06	0.18		-0.27	0.29	0.45	0.07	-0.47	-0.04	1.00
CHAN COBBLE	0.34	-0.31	0.02	0.16	0.14	0.23		0.23	-0.14	-0.10	-0.21	0.21	0.21	0.21
CHAN GRAVEL	-0.05	-0.30	0.24	0.07	0.07	0.01		0.07	-0.14	-0.25	0.09	0.28	0.28	-0.01
CHAN SAND	-0.18	0.40	-0.23	-0.32	-0.14	-0.34		0.00	-0.01	-0.13	0.00	0.06	0.06	-0.10
PLOT SCALE														
BANK	-0.14	0.19	-0.04	-0.09	-0.13	-0.04		-0.23	0.37	0.37	0.11	-0.39	-0.21	-0.21
FLOODPLAIN	-0.01	-0.04	0.04	-0.17	0.13	-0.14		0.00	-0.07	-0.10	-0.09	0.12	0.00	0.00
TERRACE	0.09	-0.20	0.11	0.11	-0.02	0.07		0.17	-0.29	-0.29	-0.09	0.29	0.15	0.15
%CLAY	-0.20	-0.12	0.39	0.25	-0.13	-0.06		0.05	-0.14	-0.15	0.19	0.05	-0.08	-0.08
%SILT	-0.14	-0.05	0.26	0.11	-0.13	-0.14		0.02	-0.09	-0.09	0.13	0.01	-0.06	-0.06
COARSE ABOVEH ₂ O	0.13	-0.15	-0.03	-0.12	0.19	0.07		-0.01	-0.02	0.03	-0.11	0.09	0.07	0.07
% LITTER	0.32	-0.17	-0.13	0.07	0.03	0.20		0.17	-0.03	0.02	-0.08	0.09	0.12	0.12
BARE	-0.08	0.02	0.08	0.00	-0.16	-0.07		0.02	0.04	-0.26	0.05	0.11	0.02	0.02
RIPBOULDER	0.19	-0.16	-0.12	-0.03	0.07	0.07		0.26	-0.12	-0.01	0.03	0.11	0.02	0.02
RIPCOGRAV	-0.24	0.31	0.00	0.06	-0.01	-0.08		-0.30	0.13	0.37	0.20	-0.44	-0.23	-0.23
	0.21	-0.29	0.01	0.05	0.24	0.22		0.23	-0.19	-0.08	-0.11	0.26	0.09	0.09

TABLE 3. Continued.

	CHAN BOULDER	CHAN COBBLE	CHAN GRAVEL	CHAN SAND	PLOT SCALE	BANK	FLOOD-PLAIN	TERRACE	%CLAY	%SILT	COARSE	ABOVE-H ₂ O LITTER	BARE	RIP-BOULDER	RIP-GRAVEL
BROAD SCALE															
TILL															
GRANITE															
VOLCANIC															
PPT															
FLOW DIRECTION															
GLACIATED															
REACH SCALE															
VALWIDTH															
V-SHAPE VAL															
VAL GRADIENT															
ELEVATION															
SINUOSITY															
CHAN WIDTH	1.00														
CHAN BOULDER	-0.03	1.00													
CHAN COBBLE	-0.47	-0.30	1.00												
CHAN GRAVEL	-0.43	-0.42	-0.30	1.00											
CHAN SAND															
PLOT SCALE															
BANK	0.37	-0.10	-0.25	-0.03		1.00									
FLOODPLAIN	-0.16	0.14	0.03	0.02		-0.30	1.00								
TERRACE	-0.29	0.02	0.25	0.03		-0.70	-0.25	1.00							
%CLAY	-0.24	-0.03	0.29	-0.06		-0.24	-0.19	0.34							
%SILT	-0.23	-0.05	0.24	0.01		-0.32	-0.11	0.36	1.00						
COARSE	-0.02	0.12	0.06	-0.12		0.20	0.27	-0.32	-0.34	1.00					
ABOVEH ₂ O	0.18	0.06	-0.12	-0.08		-0.14	-0.31	0.40	0.00	-0.02	-0.16	1.00			
% LITTER	-0.23	-0.13	0.13	0.17		-0.31	-0.25	0.45	0.44	0.40	-0.34	0.21	1.00		
BARE	0.00	0.05	-0.02	0.01		0.15	-0.02	-0.18	-0.26	-0.28	0.06	0.04	1.00		
RIPBOULDER	0.37	-0.06	-0.17	-0.14		0.33	-0.13	-0.22	-0.16	-0.16	0.05	0.01	0.05	1.00	
RIPCOBGRV	-0.13	0.17	0.18	-0.17		-0.02	0.47	-0.26	-0.29	-0.31	0.44	-0.22	0.33	—	1.00

TABLE 4. Plant composition of species groups.

Group	Species
(1) <i>RIBES-RUBUS</i>	
Mountain maple	<i>Acer glabrum</i> ssp. <i>torreyi</i>
Sierra currant	<i>Ribes nevadense</i>
Scouler's willow	<i>Salix scouleriana</i>
Creeping snowberry	<i>Symphoricarpos mollis</i>
Bracken fern	<i>Pteridium aquilinum</i>
Western thimbleberry	<i>Rubus parviflorus</i>
(2) <i>MIMULUS-ATHYRIUM</i>	
Alpine lily	<i>Lilium parvum</i>
Bittercress	<i>Cardamine cordifolia</i>
Violet spp.	<i>Viola</i> spp.
Lady fern	<i>Athyrium filix-femina</i>
Goose grass	<i>Galium aparine</i>
Bishop's cap	<i>Mitella breweri</i>
Mannagrass	<i>Glyceria elata</i>
Musk monkey flower	<i>Mimulus moschatus</i>
Cow parsnip	<i>Heracleum lanatum</i>
(3) <i>VERATRUM-POA</i>	
Kentucky bluegrass	<i>Poa pratensis</i>
Corn lily	<i>Veratrum californicum</i>
Lodgepole pine	<i>Pinus contorta</i>
Mountain gooseberry	<i>Ribes montigenum</i>
Black cottonwood	<i>Populus balsamifera</i>
Oniongrass	<i>Melica harfordii</i>
Cinquefoil	<i>Potentilla glandulosa</i>
(4) <i>SALIX-CAREX</i>	
Sedge	<i>Carex nebrascensis</i>
Lemon's willow	<i>Salix lemmonii</i>
Sedge	<i>Carex nervina</i>
Large-leaved lupine	<i>Lupinus polyphyllus</i>
(5) <i>SIDALCEA-HORDEUM</i>	
Blue wild rye	<i>Elymus glaucus</i>
Meadow barley	<i>Hordeum brachyantherum</i>
Long-leaved clover	<i>Trifolium longipes</i>
Checkerbloom	<i>Sidalcea oregana</i>
Willow herb	<i>Epilobium glaberrimum</i>
Western buttercup	<i>Ranunculus occidentalis</i>
Aster	<i>Aster occidentalis</i>

Sidalcea-Hordeum group (group 5). Species of the *Mimulus-Athyrium* group (group 2) occurred on shady stream banks and floodplains of small streams.

We identified those environmental variables with significant simple correlations with the DCA scores for each DCA axis using Pearson's correlation (r). Through stepwise multiple regression analysis we selected the significantly correlated environmental variables that most efficiently explained variation in each set of axis scores (Table 5). Seven variables explained 47% of the variation in axis 1 scores; 6 variables explained 33% of the variation in axis 2 scores. To better compare these results with those from the PCA, we plotted the Pearson's r values between each variable and axes 1 and

2 and overlaid them (Fig. 3). Like PCA axis 1, the DCA axis 1 reflected a gradient of sites that range from terraces along wide, sinuous valleys to banks along narrow, steep valleys. However, parent material and glaciation history were not significantly correlated with the DCA axis 1, as they were with PCA axis 1. DCA axis 2 is less similar to PCA axis 2: soil texture variables, which are important correlates of PCA axis 2, were not correlated with DCA axis 2.

Correlations between Riparian Vegetation and the Physical Environment

We used canonical correspondence analysis (CCA) to explore direct correlations between the occurrence of plant species and environmental factors. Axes 1 and 2 reflect high species-environment correlations ($r_{\text{axis 1}} = 0.875$, $r_{\text{axis 2}} = 0.847$; Table 6). Monte Carlo permutation tests (100 permutations; Jongman et al. 1995) show that all 3 axes were significant at $P \leq 0.01$ (see Table 6). However, the first 3 CCA axes only explained 9.9% of the total variation in species data. Monte Carlo tests indicated that species-environment relationships reflected in the first 2 canonical ordinations were significant ($P \leq 0.04$ for axes 1, 2, and 3; Table 6). Through forward selection we identified 10 environmental variables that explained the greatest percentage of species variation among the 144 sites. These variables were (in order of importance) community width, channel sinuosity, stream flow direction, parent material, channel width, elevation of riparian surface above stream level, geofluvial surface, elevation, soil texture, and average annual precipitation. Together these variables explained 95% of species variation covered by the full set of environmental variables. A CCA biplot of the 144 sites is presented in Fig. 4. Like the first PCA and DCA axes, CCA axis 1 (eigenvalue = 0.433) ordinated the plots along a gradient of riparian areas in wide valleys, with winding, shallowly sloped streams and rich soils, to areas along steep, bouldery reaches in narrow, V-shaped valleys. CCA axis 2 reflects a more muddled gradient of both valley form and soil characteristics (eigenvalue = 0.313).

Finally, we estimated the strength of fit between vegetation and remotely collected variables (parent material, glaciation history, elevation, valley width and shape, and stream flow

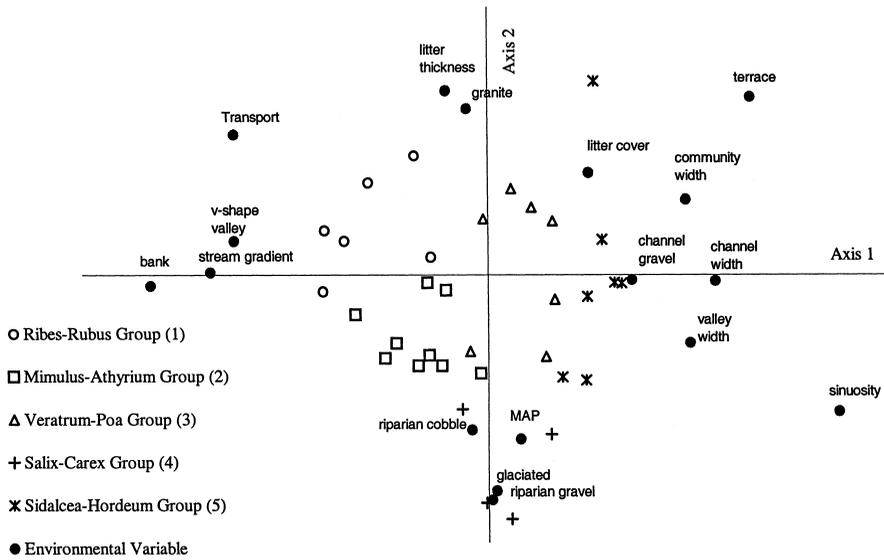


Fig. 3. Scatterplot of indicator species groups along DCA axes 1 and 2 shown with scatterplot of environmental variables. Environmental variables are plotted as Pearson's correlation (r) with sample DCA axes values. Scales for indicator species and environmental variables are different to minimize overlap for clear reading. The environmental variables are plotted on scale of -0.3 to $+0.3$, whereas the species scores are plotted on a scale of -1.0 to $+1.0$.

TABLE 5. Summary of correlations (absolute values of Pearson's r) between DCA axes and environmental variables.

Axis 1 ^a		Axis 2 ^b	
Environmental variables	abs r	Environmental variables	abs r
Sinuosity	0.26	Riparian gravel	0.13
Bank	0.25	Glaciated	0.12
Stream gradient	0.21	Litter thickness	0.10
Terrace	0.20	Terrace	0.10
V-shape	0.19	Granitic parent material	0.09
Transport	0.19	Precipitation	0.09
Channel width	0.17	Riparian cobble	0.09
Valley width	0.15	Transport	0.08
Riparian boulder	0.15	Sinuosity	0.08
Community width	0.15	Litter	0.06

^aEigenvalue = 0.57, segment length = 4.662.

^bEigenvalue = 0.44, segment length = 4.483.

direction and gradient) using the Monte Carlo permutation procedure for CCA. Monte Carlo simulations of CCA using only these environmental variables showed that the species-environment relationship was highly significant ($P = 0.02, 0.01,$ and 0.01 for axis 1, 2, and 3, respectively; Table 6).

DISCUSSION

Through multivariate analysis of environmental variables (PCA), vegetation data (DCA),

and the combined relationship between the environment and vegetation data (CCA), we consistently found that the greatest amount of variation in riparian physical structure and floristic composition occurs along a gradient of decreasing valley width, decreasing stream sinuosity, and increasing stream slope (see axis 1 in Figs. 2, 3, and 4). Thus, the same set of variables appear to control the greatest amount of variation in both the physical and vegetative characteristics of montane riparian zones. Our findings support those of Harris (1988), who found

TABLE 6. Results of canonical correspondence analysis.

Analysis	Axis 1	Axis 2	Axis 3
ALL ENVIRONMENTAL VARIABLES INCLUDED			
Eigenvalues	0.433	0.313	0.285
Species-environment Pearson correlation	0.875	0.847	0.874
Monte Carlo tests (<i>P</i> -values)			
Eigenvalue of axes	0.010	0.010	0.010
Species-environment correlation	0.040	0.040	0.010
ONLY VALLEY FORM VARIABLES INCLUDED WITH SPECIES DATA ^a			
Eigenvalues	0.291	0.249	0.175
Species-environment Pearson correlation	0.757	0.811	0.742
Monte Carlo tests (<i>P</i> -values)			
Eigenvalue of axes	0.010	0.010	0.010
Species-environment correlation	0.020	0.010	0.010

^aValley form variables include variables that could be collected in a GIS without site visits: parent material, glacial history, elevation, valley width, valley shape, stream flow direction, and stream gradient.

that riparian vegetation was correlated to valley-bottom shape in the eastern Sierra Nevada. Although surface variables (e.g., gravel cover, litter thickness, soil organic matter content, and percent bare ground) are also an important source of variation in the physical composition of the riparian zones, they did not emerge as important correlates to plant species distribution. Instead, the 2nd DCA and CCA axes present more muddled gradients related to precipitation, parent material, and surface conditions. The differences among the 2nd axes show that there is a gradient in surface conditions not reflected in the vegetation. This difference offers the interesting interpretation that riparian plant species distribution might be less controlled by surface conditions than by other, broader scale factors. Since the 2nd DCA and CCA ordination axes were poorly correlated with a clear environmental gradient and actually from one another, it is likely that some indirectly or altogether unmeasured variable(s), such as disturbance regime or seasonal groundwater levels, have an important fine-tuning effect on riparian plant species distribution.

Correlations between Riparian Vegetation and the Physical Environment

As stated above, variables associated with stream valley form (channel sinuosity, channel width, and parent material) explain the greatest amount of variation in plant species distribution (Figs. 3, 4). Valley form incorporates several variables that are likely to directly affect plant establishment and survival. These include insolation and temperature; distur-

bance type and frequency; and depth to, and seasonal shifts in, the groundwater table. Thus, species that require full sun are found in wide, flat valleys (e.g., the *Sidalcea-Hordeum* group). Species that are shade-tolerant but have high water requirements are found in V-shaped valleys close to the water's edge or on mid- and upper banks in areas that receive the highest precipitation in the LTB (e.g., the *Mimulus-Athyrium* group).

Given results from past studies, our findings that plant species distribution was not highly correlated with surface conditions were somewhat surprising. For example, Sollers (1974) reports that in the lower 50 miles of Wissahickion Creek, riparian vegetation patterns correlated with surface soil type, which in turn was correlated with site channel dynamics. However, our survey differs from that of Sollers and of many others because we incorporated the full length of streams in our study and included the source and transport as well as the depositional reaches. Thus, large differences in light, temperature, and disturbance regime associated with watershed position could have overwhelmed effects due to differences in surface conditions. In addition riparian areas subject to frequent scouring (rather than deposition) might select for opportunistic species capable of germinating and growing quickly or species capable of withstanding scouring floods, rather than selecting for species that are superior competitors under specific soil and site conditions (e.g., Grime 1988). Finally, we did not measure soil conditions at depth (below 10 cm), and variables such as rooting depth and depth to saturation (or signs thereof) have been reported

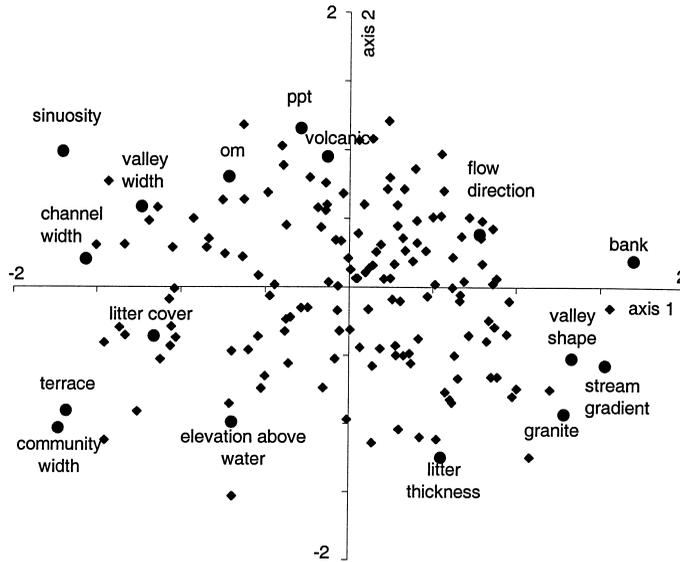


Fig. 4. Canonical correspondence analysis biplot of 144 plots in LTB (◆). Positions of environmental variables with correlations to axes that are greater than 0.20 are also shown with (●).

as important indicators of plant species composition in meadows of the Great Basin (Weixelman et al. 1997).

The first 3 CCA axes explained one-tenth (9.9%) of the variation in species composition in the 144 riparian plots (Table 6). This value is low compared to other studies in upland areas where CCA axes captured 15%–25% of variation in site species composition (e.g., Brown et al. 1993, Rydgren 1996). To some extent this low correlation could result from a high degree of stochasticity that affects plant species distribution in riparian environments, or it could be due to the small plot size used in this study. However, dissimilarities between scatterplots of the constrained (CCA) and unconstrained (DCA) ordination scores indicate that some important environmental variables might have been missing from the constrained ordination. In particular, measurements of flooding disturbance regime and water availability might have increased the amount of variation captured by CCA axes. In many bottomland systems, riparian plant species distribution has been correlated to groundwater levels and flood frequency and duration (Hack and Goodlett 1960, Sigafos 1961, Hupp 1992). These factors have also been cited as major correlates with riparian sediment moisture and texture (Hack 1957, Osterkamp and Hupp 1984). Although several variables we

measured might be correlated to disturbance regime and water availability (e.g., elevation above bank-full, channel width, elevation, and geofluvial surface), the distribution of vegetation in relation to response and recovery from disturbance might be more clearly revealed through direct measures of disturbance history (Sprugal 1991, Hobbs and Huenneke 1992) and stream power (Bendix 1994) than through the variables measured herein. Other abiotic characteristics not included in this study, such as measures of rooting depth, soil chemistry, and subsurface hydrology, might also provide important, direct measures of factors controlling plant species distribution (Weixelman et al. 1997).

Our results demonstrate that plant species composition in the LTB riparian zones can vary from areas dominated by shrubs to areas dominated by grasses and herbs to areas occupied primarily by willows, sedges, and herbs. The broad range in species composition reflected in the DCA axes (>4.0 standard deviations) could result in large differences in biotic potentials, and therefore ecosystem processes, among sites. Thus, the combination of floristic and structural variation summarized along the 1st PCA and DCA ordination axes are likely to reflect an associated diversity of ecosystem processes. Ecosystem processes likely to be correlated to variation described in the first 2

axes include sediment and nutrient dynamics, and dispersion and support of diverse plant and animal species.

Hierarchy Theory and Scales of Control over Riparian Structure

In this study we found strong correlations among physical variables at different scales; these results support the concept that the physical structure of montane riparian systems is constrained by a spatial hierarchy of landscape elements. Barnes et al. (1982), who worked in uplands, and Kovalchik (1987), who worked in riparian zones, both suggest using coarse-scale differences in climate and parent material to hierarchically organize landscapes for ecosystem classification. Kovalchik (1987) further suggests organizing areas homogeneous in climate and parent material into subsidiary units based on differences in valley form. Tabacchi et al. (1998) summarized much of the theory and literature on riparian and watershed ecology when they stated that bedrock geology, geomorphic features, soil characteristics, climate, and hydrologic regime are the primary factors influencing formation of the riparian zone. Results from our work support current theory on factors that control riparian development. For example, strong correlations between parent material and valley form suggest that parent material affects valley shape and gradient. At a finer scale in the hierarchy, geofluvial surface and surface soil texture are highly correlated; these correlations support the interpretation that geofluvial surface constrains soil formation and composition. We found significant correlations that suggest a link between valley form and geofluvial surface. In particular, banks without associated terraces were the most common surface type along steep, narrow stream valleys; and terrace frequency increased in wider, low-gradient reaches. These correlations suggest that a hierarchy of physical factors control the abiotic structure of LTB riparian zones. According to this scheme, parent material and glaciation history constrain the width, shape, and gradient of stream valleys; and stream-valley form effects the distribution of geofluvial surfaces. In turn, geofluvial surface constrains surface conditions (Fig. 5).

Results from this research indicate that variation in riparian plant composition is constrained by the 1st several layers of this hierar-

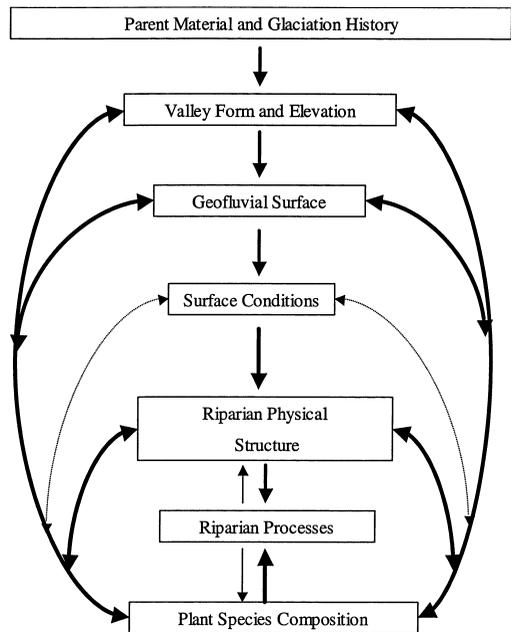


Fig. 5. Proposed hierarchy of constraints for the physical structure and plant species composition of riparian zones in LTB. Physical variables that occur at the upper levels of the hierarchy have greater influence on plant species composition than finer scale variables, such as surface conditions. The figure also indicates that both physical structure and biotic components of the riparian zone can constrain ecological processes.

chy where coarse-scale, abiotic constraints are predicted to dominate (e.g., CCA axis 1; also see Fig. 5). The effects of physical constraints on plant species composition weakens at spatial scales finer than the geofluvial surface. In the montane landscape, large differences in valley shape (valley form, gradient, sinuosity) effect large differences in site insolation and disturbance regime. It seems likely that the dominance of these coarse- to moderate-scale variables on plant community composition over the finer scale variables related to site surface conditions reflects the overwhelming importance of light and disturbance regime on montane riparian community composition. These results suggest that it might be useful to use these coarse- to moderate-scale data to model the distribution of montane riparian ecosystem types; however, the large amount of variation in plant species composition that was unexplained by the variables collected indicate that other variables, such as disturbance regime, might be necessary to make such models truly informative.

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