Distribution of herbs and shrubs in relation to landform and canopy cover in riparian forests of coastal Oregon

Robert J. Pabst and Thomas A. Spies

Abstract: In this study we characterized the distribution of herb and shrub species relative to landform and forest canopy attributes of streamside forests in the moist, conifer-dominated mountains of coastal Oregon. Species cover and environmental data were collected along transects at 94 sites. Species with relatively similar distributions were classified into 10 species groups to identify major patterns in the vegetation. Although these patterns were highly variable, ordination and gradient analyses indicated that vegetation composition is ordered along a complex environmental gradient running from streamside to hillslope. Similarly, species diversity followed a decreasing trend from active fluvial surfaces to lower hillslopes. Vegetation patterns were related to specific landforms, topographic positions, microsites, and coniferous tree cover within the trans-riparian gradient. We hypothesize that the environmental features correlated with these patterns are surrogates for the underlying mechanisms responsible for them. These are (*i*) hillslope processes and associated moisture gradients; (*ii*) hydrological disturbance; (*iii*) tolerance of saturated, valley-floor soils; (*iv*) shade tolerance; and (*v*) mineral soil disturbance. This study indicates that valley-floor and lower-slope plant communities are distinct elements in these forest landscapes, supporting the assumption that riparian zones require a different management and conservation strategy than upland forest communities.

Key words: riparian vegetation, ordination, gradient analysis, species groups, landform.
Nomenclature is based on that of Hitchcock and Cronquist (1973).

Résumé : Dans leur étude, les auteurs caractérisent la distribution des espèces herbacées et arbustives selon les aspects de la forme du relief et de la canopée forestière, dans les forêts humides voisinant les rivières des montagnes côtières de l'Oregon, dominées par les conifères. Ils ont récolté des données sur la couverture en espèces et sur l'environnement le long de transects, sur 94 sites. Les espèces ayant des distributions relativement similaires ont été réunies en 10 groupes d'espèces, pour identifier les patrons majeurs de végétation. Alors que ces patrons sont très variables, les analyses par ordination et gradient indiquent que la composition de la végétation est ordonnée selon un gradient environnemental complexe allant du bord des rivières vers les pentes des montagnes. De la même façon, la diversité en espèces suit une tendance décroissante, des surfaces fluviales actives vers les pentes montagneuses. Les patrons de végétation sont reliés aux formes de relief spécifiques, aux positions topographiques, aux microsites et à la couverture par les conifères, à l'intérieur du gradient trans-riparien. Les auteurs formulent l'hypothèse que les caractéristiques environnementales corrélées avec ces patrons sont des substituts pour les mécanismes sous-jacents qui en sont responsables. Ce sont : (*i*) les processus liés à la pente et associés aux gradients d'humidité; (*ii*) la perturbation hydrologique; (*iii*) la tolérance du sol saturé du fond de la vallée; (*iv*) la tolérance à l'ombre; et (*v*) la perturbation du sol minéral. Cette étude indique que les communautés végétales du fond de la vallée et des bas de pente sont des éléments distincts dans ces paysages forestiers, ce qui supporte la proposition que les zones ripariennes nécessitent un aménagement et une stratégie de conservation différents par rapport aux communautés forestières en altitude.

Mots clés : végétation riparienne, ordination, analyse de gradient, groupes d'espèces, forme de relief.

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Introduction

Ecologists have given considerable attention to the organization and distribution of plant communities in riparian zones. For example, the association between vegetation patterns and fluvial processes is well documented for many areas of North America (Hack and Goodlett 1960; Fonda 1974; Hawk and Zobel 1974; Campbell and Franklin 1979; Swanson and Lienkaemper 1982; Hupp 1983; Osterkamp and Hupp 1984; Hupp and Osterkamp 1985; Harris 1987, 1988; Baker 1989;

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Kovalchik and Chitwood 1990; Gregory et al. 1991; Rot 1995; Walford and Baker 1995). Most of these studies were done either in dry climates, where riparian zones are unique landscape elements (Malanson 1993), or in stream systems with broad, well-developed floodplains. Exceptions include Hack and Goodlett (1960) in the Appalachian Mountains, Campbell and Franklin (1979) in the Oregon Cascades, and Rot (1995) in the Washington Cascades. For the most part, however, not much is known about riparian and lower-slope vegetation along narrow, mountain streams in moist, temperate climates. In these settings, exemplified in the coastal mountains of western North America, the distinction between streamside and upland vegetation may be obscured by low moisture gradients and fluvial processes (e.g., erosion, flooding, channel migration, sediment deposition) that are constrained by surrounding topography. It is believed that community patterns and biological diversity along mountain streams are organized by landforms created through geomorphic processes (Gregory et al. 1991), yet it is not clear if these relationships hold where landforms and fluvial surfaces are spatially compressed, closely juxtaposed, and naturally fragmented. Species distribution also may be affected by fluvial disturbance (Hupp and Osterkamp 1985; Harris 1988), hillslope failure (Gregory et al. 1991), differences in shade tolerance (Menges and Waller 1983), canopy (litter) type (Franklin et al. 1968; Fonda 1974), and competition for germination sites (Walker et al. 1986). In light of the many factors that can influence species distribution, to what extent do discrete vegetation patterns exist in riparian areas of steep mountain ecosystems?

We examined this question in the Coast Range of Oregon, where only a few studies have been done on riparian vegetation. Hemstrom and Logan (1986) described 23 plant associations in relation to soils, topography, and climate to guide management planning on a national forest. Four of these associations incorporated riparian and lower-slope settings. These authors proposed various successional pathways involving the development of salmonberry (*Rubus spectabilis* (Pursh)) and red alder (*Alnus rubra* (Bong.)), two species that are prevalent in Coast Range riparian areas. The "red alder/salmonberry habitat type" was studied by Henderson (1978) using a chronosequence of stand ages to describe changes in species composition and abundance over time. He theorized that salmonberry could become the dominant feature of a climax riparian plant community. Hibbs and Giordano (1996) found no significant differences in herbaceous species diversity between alder-dominated riparian buffer strips and undisturbed red alder stands. Woody plants were the focus of Minore and Weatherly (1994), who correlated the distribution of riparian shrubs and tree regeneration with proximity to streams, topography, and overstory tree composition. These studies have provided valuable information on Coast Range riparian vegetation. To date, however, what has been lacking for the Coast Range, as for most of the coastal Pacific Northwest, is an extensive description of herb and shrub patterns in riparian and lower-slope forests.

Thus, the objectives of this study were to (*i*) characterize the composition, distribution, and diversity of herb and shrub species in riparian forests of the central Coast Range of Oregon; (*ii*) identify assemblages or groups of species occurring together on a consistent basis throughout the study area; and (*iii*) relate the distribution of these groups and selected individual species to landforms, forest canopy attributes, and other environmental features. In theory, species with similar distributions along compositional or environmental gradients can be grouped to help elucidate vegetation–environment relationships (Pregitzer and Barnes 1982; Spies and Barnes 1985*a*; Halpern 1989). Species groups also can facilitate rapid assessments and mapping of community types or ecological land classification units (Barnes et al. 1982; Spies and Barnes 1985*b*). For ecosystems as dynamic and spatially heterogeneous as riparian areas, species groups may be more useful for understanding ecological patterns and identifying ecological management units than a broad classification based on climax or potential natural vegetation types. The species group approach seemed particularly appropriate after our initial work in these areas showed a high degree of fine-scale complexity and spatial heterogeneity in species distribution.

Methods

Study area

Study sites were located in the central Coast Range of Oregon between 44.2 and 44.6°N latitude and 123.4 and 124.1°W longitude, primarily within the watershed of the Alsea River (Fig. 1). Total annual precipitation in the study area is associated with distance from the Pacific Ocean: along the coast it averages about 200 cm, increases to more than 250 cm in the west-central Coast Range, and then declines to about 150 cm along the eastern fringe (U.S. Weather Bureau 1960). Precipitation occurs primarily as rain from October through April, although fog drip during summer months can be substantial along the coast (Azevedo and Morgan 1974). Temperatures are moderate, with January mean minima ranging from 0–3°C and August mean maxima ranging from 18–26°C; the difference between mean summer highs and winter lows is somewhat greater with increasing distance from the ocean (Oregon Climate Service 1997). Most of the study area is underlain by uplifted marine sediment (Franklin and Dyrness 1973). Some sites in the eastern Coast Range overlay igneous intrusions, and some coastal sites are on basalt flows. Elevations range from near sea level to about 1250 m, but most ridge tops are less than 700 m.

The entire study area is deeply dissected by a dense network of perennial and intermittent stream channels (Fig. 1, inset). Streamflow regimes closely track precipitation patterns, with peak flows in winter and low flows in late summer or early autumn. Peak flows recorded over a 55-year period on the Alsea River ranged from 243 to 1183 m^3/s, while low flows ranged from 1.3 to 3.2 m^3/s (U.S. Geological Survey 1997). There were 21 flood events during that time. Mean discharge was around 41 m^3/s on the Alsea River (U.S. Geological Survey 1997), a sixth-order stream. Average discharges on two third-order streams in the study area ranged from 0.1 to 0.2 m^3/s; maximum discharges ranged from 3.9 to 5.7 m^3/s (Moffatt et al. 1990).

Two major vegetation types are represented in the study area. The western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) zone occupies the majority of the Coast Range, while the Sitka spruce (*Picea sitchensis* (Bong.) Carr.) zone is confined to a narrow band (the "fog belt") along the coast (Franklin and Dyrness 1973). Overstory tree composition generally is related to topographic position (Hemstrom and Logan 1986), with slopes occupied by densely growing conifers (primarily Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western hemlock), and valley floors occupied by scattered to frequent deciduous hardwoods (red alder and bigleaf maple (*Acer macrophyllum* Pursh)) or mixed patches of hardwoods and conifers.

Study sites

Data were collected from June to September in 1989 and 1990 at 94

Table 1. Means and ranges (in parentheses) of study site characteristics by stream order.

Stream order	No. of sites	Valley-floor width (m)	Stream bankfull width (m)	Stream channel gradient (degrees)	Elevation (m)	Distance from coast (km)
1	16	11.0 (0.7–49.3)	2.7 (0.7–4.6)	12.6 (4.0–23.7)	304.0 (122–610)	26.6 (4.8–46.7)
2	40	25.3 (5.3–83.7)	4.3 (2.0–8.5)	3.7 (1.0–8.3)	197.0 (49–365)	28.5 (10.7–45.4)
3	30	35.8 (6.5–95.6)	7.9 (4.8–14.3)	2.9 (1.0–8.3)	180.6 (37–330)	24.9 (1.6–50.6)
4	3	78.8 (69.0–87.8)	18.3 (9.6–23.0)	1.4 (0.7–2.0)	219.7 (122–293)	27.6 (8.0–38.1)
5	5	91.8 (20.4–135.4)	23.8 (18.5–32.7)	1.1 (0.7–1.5)	64.0 (49–73)	18.6 (11.9–30.0)

Fig. 1. Study sites (n = 94) in the central Coast Range of Oregon. ○, one side of stream sampled; ▲, both sides of stream sampled.

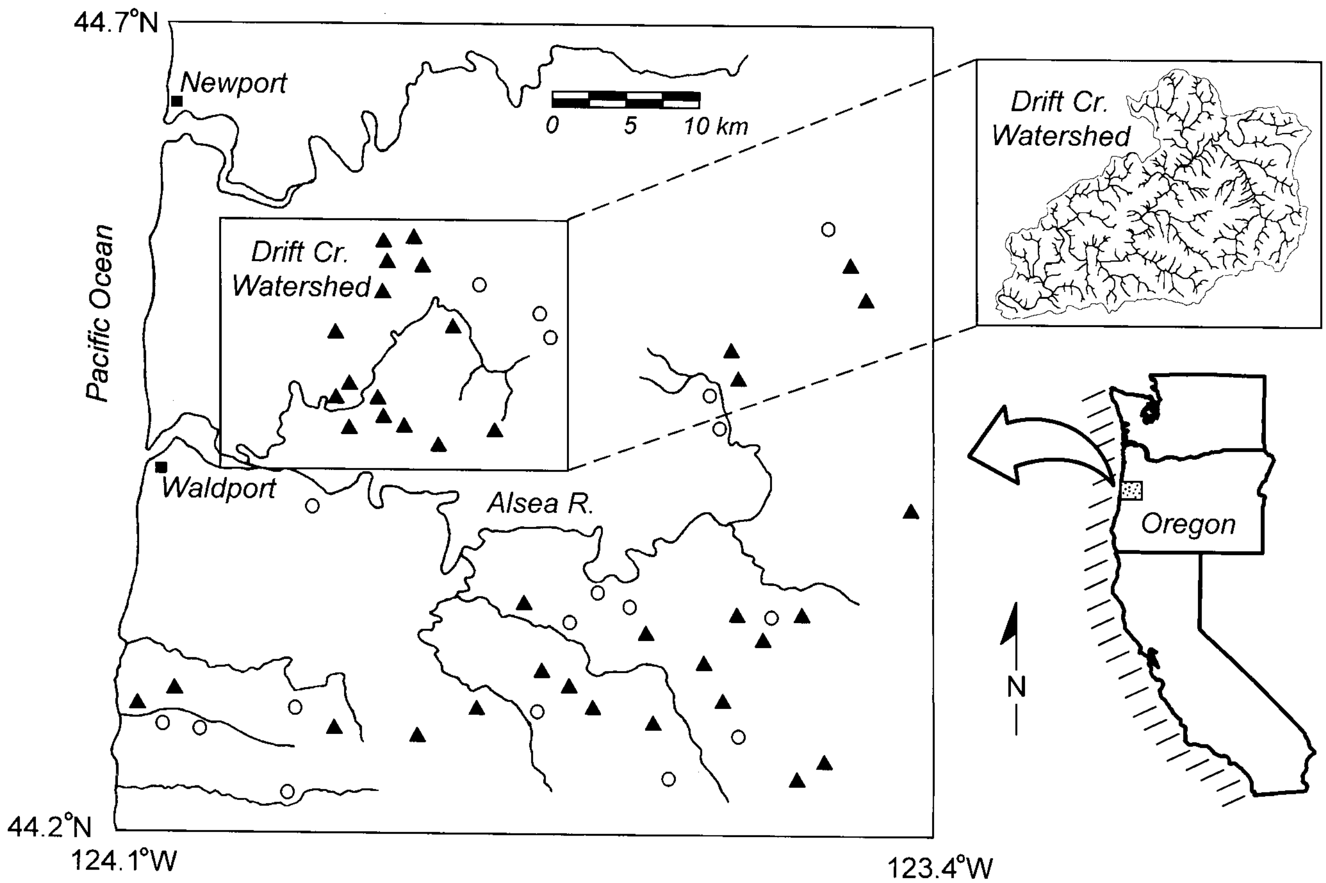


Fig. 2. Schematic of a Coast Range riparian area showing landforms, topographic positions, and microsites.

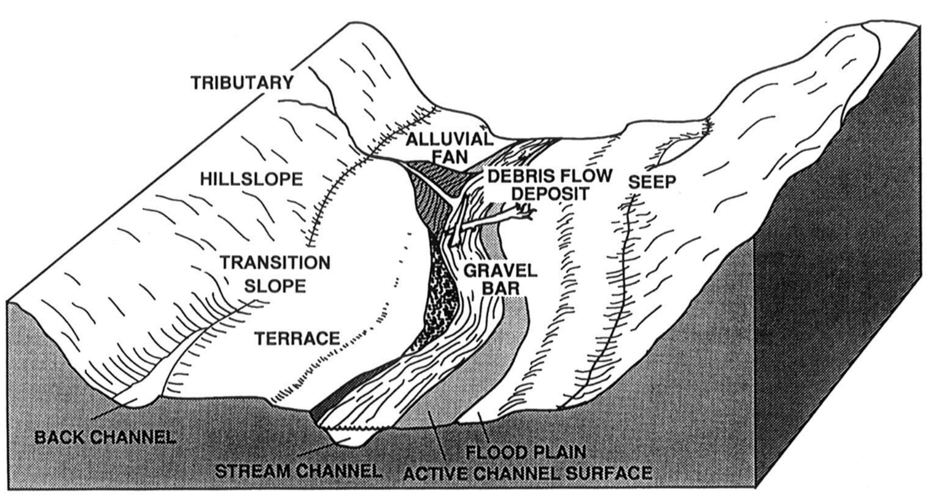


Table 2. Means and ranges (in parentheses) for physical features of major landforms and topographic positions.

Landform or topographic position	Number sampled	Height above stream (m)	Distance from stream (m)	Slope (degrees)
Floodplain	45	0.3 (0.0–1.2)	1.0 (–1.9–3.6)	7.8 (0–25)
Terrace	83	1.0 (0.0–6.3)	6.3 (0.5–28.0)	7.6 (1–27)
Transition slope	94	2.3 (0.4–8.5)	14.7 (2.0–79.9)	27.8 (5–48)
Lower hillslope	93	10.8 (2.8–19.7)	31.3 (9.5–113.6)	29.4 (4–48)

Note: Distance from stream was measured from the edge of the bankfull channel. Vegetated flood plains located between the bankfull and low-flow channels had negative values for distance.

Table 3. Environmental variables used in analysis of riparian vegetation patterns.

Site level	Transect level	Plot level	Subplot level
Elevation (m)	Valley-floor width (m)	Landform or topographic position	Tall-shrub cover (%)
Distance from ocean (km)	Bankfull width of stream (m)	Slope (degrees)	Deciduous tree cover (%)
Age of dominant trees on valley floor (years)	Stream channel gradient (degrees)	Aspect (degrees)	Coniferous tree cover (%)
Age of dominant trees on hillslope (years)	Direction of streamflow (degrees)	Distance from stream (m)	Open sky cover (%)
Height of dominant trees on valley floor (m)	Streambed substrate (scaled from 1 to 8)	Height above stream (m)	Height of dominant shrub layer (m)
Height of dominant trees on hillslope (m)	Conifer tree gap over stream (area in degrees)		Extent of browsing (scaled from 0 to 3)
Stream order (scaled from 1 to 5)	Deciduous tree gap over stream (area in degrees)		Extent of burrowing (scaled from 0 to 3)

sites along 42 streams (Fig. 1). A site was defined as the area from the stream to the lower hillslope along one side of a 100-m reach of stream. Each stream reach sampled was relatively uniform in valley-floor width and overstory type. We selected sites from aerial photographs and field reconnaissance to sample a range of stream orders (first through fifth) (Horton 1945), valley-floor widths, overstory types (coniferous, deciduous, mixed), and geographic locations within the west to east climatic gradient. Study site characteristics are summarized by stream order in Table 1.

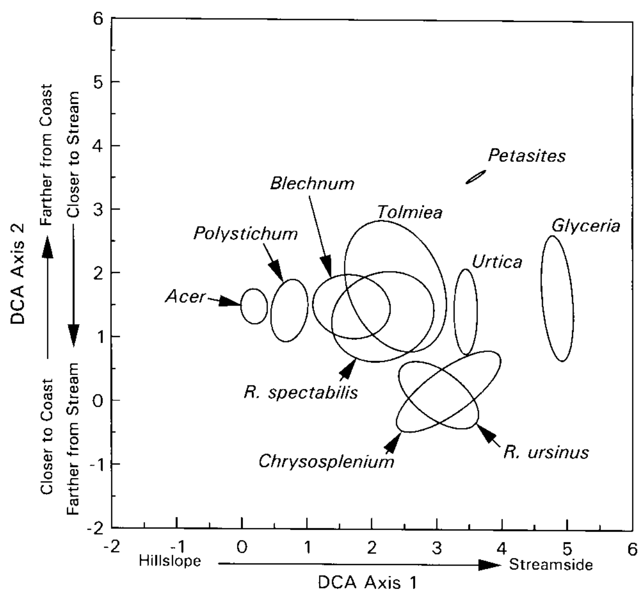
The majority of sites (80 of 94) were in unmanaged, mature forest that regenerated following stand-replacing fires. Ages of dominant upland conifers in most of these stands ranged from 80 to 140 years, although 13 of the sites were in stands that had trees older than 200 years. Ages of the oldest valley-floor trees were usually the same as those of upland trees, but at some sites they were younger, the likely result of fluvial disturbances more recent than the fires. The remaining 14 sites were in younger stands (25–80 years) that originated either naturally or by planting following tree harvest or fire. Three sites with broad valley floors had evidence of past (within 100 years) homesteading.

Data collection

At each site, we collected data in plots along two or three transects that extended from the stream edge to 24 m up the lower hillslope in a direction roughly perpendicular to streamflow. The location of the first transect was chosen randomly within the upper section of the study reach. Successive transects were 25 m apart in a downstream direction. Plots were located on major valley-floor landforms (active floodplain, terrace), the lower hillslope, and on what we term the "transition" slope (similar to Hack and Goodlett's (1960) "foot slope") just beyond the slope break between the valley floor and lower hillslope (Fig. 2). Physical features of these landforms and topographic positions are compared in Table 2. Minor landforms and valley-floor microsites, including gravel bars (distinct from the active floodplain), small-scale alluvial fans, logs, boulders, debris-flow deposits, seeps, back channels, and eroded banks, were sampled less frequently. There were a minimum of 2 and as many as 10 plots per transect, and from 5 to 29 plots per site, depending on the width of the valley floor. There were 1198 plots in all.

Percent cover of tall shrubs (>1.5 m) was estimated in 4 × 4 m plots. Cover of low shrubs, herbs, mosses (all species combined), logs (>10 cm diameter), exposed rock, and bare ground was estimated in subplots nested within plots. In 1989 we used a single subplot that was 2 × 4 m in size; in 1990 we sampled four 1 × 1 m subplots at each corner of the 4 × 4 m plot. Cover of overstory shrubs, deciduous trees, coniferous trees, and open sky was estimated from the center of each subplot using a canopy viewer (Mueller-Dombois and Ellenberg 1974) with a circular aperture of 18.5°.

Fig. 3. Arrangement of species groups in DCA space as depicted by standard deviation ellipses around weighted means of DCA species scores (weighting factor equals the proportion of species occurrences in 377 composite sample units). Directional arrows indicate important environmental gradients identified through correlation analysis.



Stream order, elevation, distance from the coast, and the age and

Table 4. Species groups of Coast Range riparian areas, with frequency of occurrence class and mean percent cover over all sample units and by sample unit location (landforms, topographic positions, and microsites).

	Overall ($n = 377$)		Sample unit location: Floodplain ($n = 45$)		Terrace ($n = 83$)		Transition slope ($n = 94$)		Hillslope ($n = 93$)		Alluvial fan ($n = 3$)	
Species group	Class	Cover (%)	Class	Cover (%)	Class	Cover (%)	Class	Cover (%)	Class	Cover (%)	Class	Cover (%)
Glyceria	4	8.5	6	24.7	6	6.0	3	1.7	2	3.0	10	0.8
Petasites	1	8.0	2	6.2	1	4.3	1	0.4	1	0.1	—	—
Urtica	3	5.0	4	5.0	5	7.2	3	1.5	2	1.3	—	—
Chrysosplenium	5	3.0	8	2.9	6	1.2	5	0.8	1	0.1	10	2.2
Tolmiea	10	20.4	10	32.5	9	27.8	10	16.9	9	5.8	10	33.0
Rubus spectabilis	10	35.7	10	32.2	10	46.5	10	41.4	10	25.0	10	39.3
Rubus ursinus	5	1.3	4	1.5	6	1.4	5	1.3	6	1.1	7	0.5
Blechnum	8	2.9	6	1.3	8	1.8	9	3.6	8	3.2	7	0.6
Polystichum	9	15.9	5	10.1	10	11.7	10	16.0	10	24.0	10	7.5
Acer circinatum	5	9.4	1	29.0	5	4.4	7	6.3	9	13.1	4	0.1

Note: Frequency classes are as follows (ranges in %): 1, 0–10; 2, 10–20; 3, 20–30; 4, 30–40; 5, 40–50; 6, 50–60; 7, 60–70; 8, 70–80; 9, 80–90; 10, 90–100. n, number of sample units.

height of representative valley-floor and hillslope trees were recorded for each site. For each transect, we recorded total valley-floor width, area of the gap in the deciduous and coniferous tree canopies over the stream, streambed substrate (wood, sediment, gravel, cobble, boulder, bedrock), bankfull width of the stream, stream channel gradient, and direction of streamflow. On every plot (i.e., landform, microsite, or topographic position), we collected data on slope, aspect, distance from stream, height above stream, height of the dominant shrub layer, and extent of animal browsing and burrowing. The entire list of environmental variables is shown in Table 3.

Data analysis

Species cover and environmental data were averaged for each landform, topographic position, or microsite at each study site. For example, data from all terrace plots at a single site were averaged to generate one "composite" sample unit. There were 377 composite samples in all; these became the basis for classification, ordination, correlation, and other descriptive analyses. Species occurring fewer than six times were dropped from classification and ordination. *Polypodium glychirrizae*, an epiphytic fern, and moss cover, which was nearly ubiquitous, were also dropped. We used two-way indicator-species analysis (TWINSPAN) (Hill 1979*a*) to classify the remaining species into groups, using pseudospecies cut levels of 0, 2, 5, 10, 20, and 40% cover; defaults were used for all other options. Environmental variables were averaged to reflect the environmental conditions associated with each species group. For each group, these means were weighted by the total percent cover of that group in each composite sample.

We used detrended correspondence analysis (DCA) (Hill 1979*b*), with default levels for all options, for ordination of the species – sample unit data matrix. DCA has been criticized for its use in gradient analysis (Minchin 1987), but we found that the results it provided were interpretable, confirmed patterns that we recognized in the field, and suggested useful ways of thinking about species–environment relationships that we had not identified previously. Interpretation of the first two DCA axes was aided by calculating Spearman rank correlations between sample unit scores and unweighted means of the 25 environmental variables. Within-species group variation and the distinctness of groups in ordination space were evaluated by generating ellipses (with axes equal to two times the standard deviation) around unweighted and weighted means of DCA species scores. The weighting factor equaled the proportion of species occurrences in the 377 composite samples, and was applied to emphasize the most frequently occurring species in each group, thereby reducing variation. A second ordination and gradient analysis was performed using cover data for just the tall-shrub species, of which there were 13. Our rationale for this was that tall shrubs are the dominant component of the understory in Coast Range riparian areas, and that patterns in their distribution may reflect overall vegetation patterns. There were 361 composite samples with tall shrubs.

We calculated species richness and diversity with Hill's indices (N0, N1, N2) (Hill 1973) using the program PRHILL (B.G. Smith, pers. comm.), and derived species–area relationships with 1990 subplot data using all plant species. For this analysis, subplots were grouped initially into three categories for comparison: valley floor, transition slope, and hillslope. Subsequently, the valley-floor data were split into two components: active channel surfaces (represented by gravel bars and floodplains) and inactive surfaces (represented by terraces and seeps).

Results

Species group classification and ordination

A total of 141 plant species were encountered, 96 of which occurred more than five times (58 forbs, 16 graminoids, 6 ferns, 3 low shrubs, and 13 tall shrubs). We assembled these 96 species into 10 groups based on interpretation of TWINSPAN output (Table 4). We reclassified some species on the basis of field observations. The groups are named for a dominant or characteristic species. Species within groups had relatively similar distributions, although in any one composite sample, species from different groups could be (and frequently were) present. In addition, species making up a single group rarely occurred all together in a composite sample.

Within-group variation in DCA species scores was large, and there was substantial overlap among groups in ordination space. Weighting group means to emphasize the most common species helped to define the groups more clearly, although some overlap still occurred (Fig. 3). The first DCA axis (eigenvalue = 0.66) represents a strong compositional and topographical gradient from hillslope to streamside, with the extremes occupied by the *Acer circinatum* and *Glyceria* groups, respectively. The variables most strongly ($p \leq 0.001$) and negatively correlated with axis 1 sample scores reflect this

Table 4. (*concluded*).

Sample unit location													
Back channel ($n = 9$)		Boulder ($n = 7$)		Debris flow ($n = 8$)		Eroded bank ($n = 11$)		Gravel bar ($n = 10$)		Log ($n = 4$)		Seep ($n = 10$)	
Class	Cover (%)	Class	Cover (%)	Class	Cover (%)	Class	Cover (%)	Class	Cover (%)	Class	Cover (%)	Class	Cover (%)
7	7.3	2	0.5	2	2.5	1	0.5	7	17.0	3	0.5	6	2.4
2	3.5	2	0.5	3	1.1	1	5.3	4	37.2	—	—	1	20.0
3	5.4	3	1.3	—	—	1	2.0	8	1.1	—	—	3	32.0
9	7.4	3	1.8	3	0.6	2	0.6	6	0.6	3	0.5	9	24.2
10	27.5	10	17.4	10	27.4	10	32.1	10	17.5	10	10.3	10	36.4
10	53.8	10	16.0	10	19.5	10	41.8	10	19.6	10	45.5	10	22.3
4	1.4	—	—	4	1.2	4	0.8	3	1.8	—	—	1	0.5
4	1.8	2	0.5	7	2.1	7	5.5	3	2.3	5	15.5	4	3.5
8	10.0	5	22.0	10	4.0	6	4.9	4	4.2	10	3.0	5	10.1
2	14.8	—	—	4	0.7	5	15.3	—	—	3	20.5	1	4.0

Table 5. Spearman rank correlation coefficients (r) between DCA scores and environmental variables for 377 composite sample units.

Environmental variable	DCA axis 1 (eigenvalue = 0.66)	DCA axis 2 (eigenvalue = 0.37)
Height above stream	–0.66	–0.33
Slope	–0.58	ns
Distance from stream	–0.54	–0.41
Percent cover conifer overstory	–0.54	ns
Shrub height	–0.39	–0.24
Percent cover shrub overstory	–0.29	–0.29
Conifer canopy gap over stream	0.22	–0.23
Percent cover open sky	0.21	ns
Stream channel gradient	–0.19	ns
Browsing	0.19	–0.27
Distance from the coast	–0.18	0.24
Elevation	ns	0.24
Animal burrowing	ns	–0.22
Valley-floor width	ns	–0.20

Note: Only variables significant at $p \leq 0.001$ for one or both axes are shown. ns, not significant at $p > 0.001$.

gradient: height above stream, slope, distance from stream, and percent cover of conifers (Table 5). In general, the *Glyceria*, *Petasites*, *Urtica*, and *Chrysosplenium* groups were restricted to valley floors, while the *Acer circinatum* and *Blechnum* groups mostly were confined to slopes. The *Tolmiea*, *Polystichum*, *Rubus ursinus*, and *Rubus spectabilis* groups were more widespread.

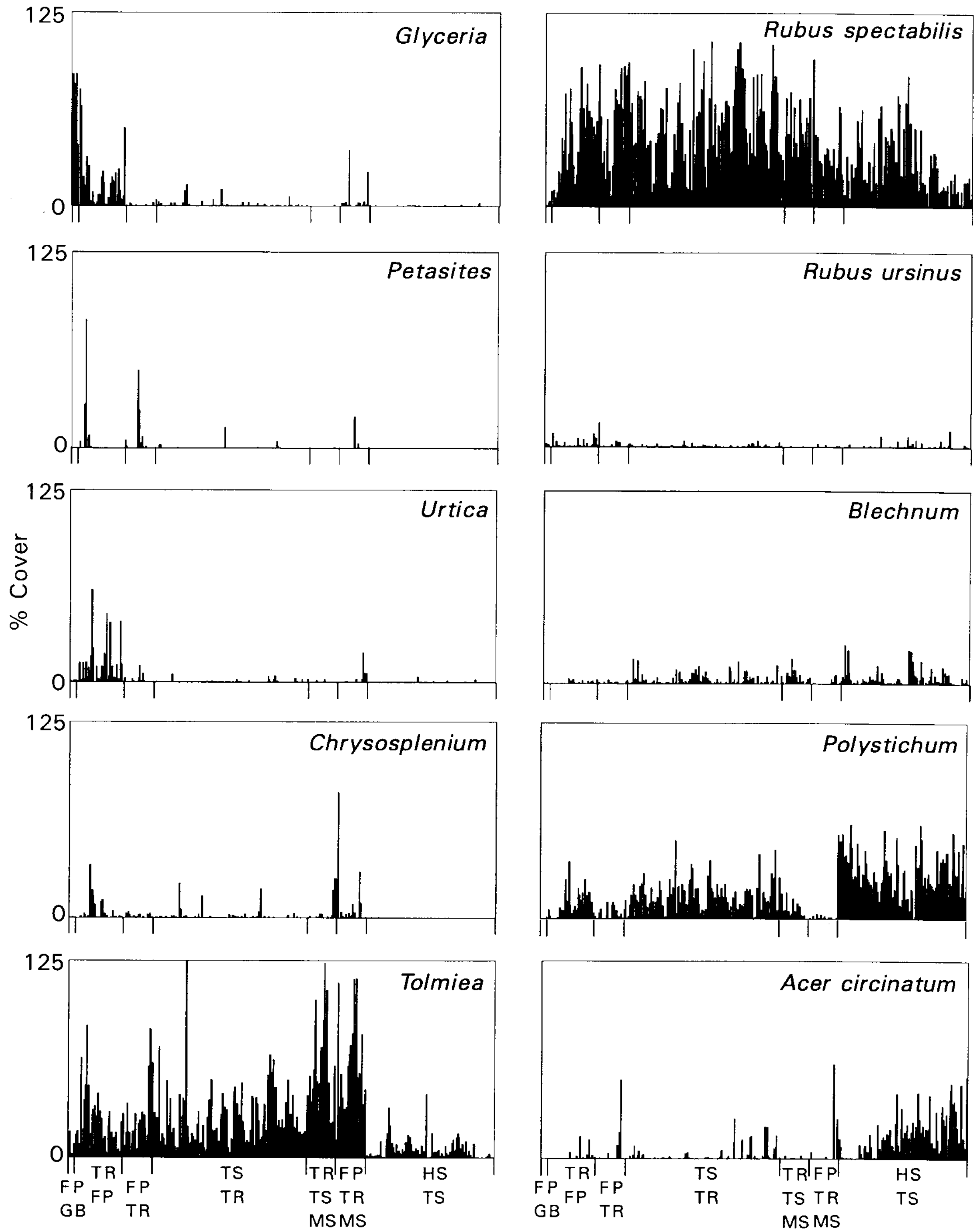
The second DCA axis (eigenvalue = 0.37) represents a complex gradient related to location within the valley floor and distance from the coast. This gradient is determined largely by the difference between the *Petasites* group, with high axis 2 scores, and the *Rubus ursinus* and *Chrysosplenium* groups, with low axis 2 scores (Fig. 3). For the *Glyceria* and *Urtica* groups, variation along axis 2 was high relative to that along axis 1; these groups were found chiefly on active channel surfaces and include opportunistic species that are tolerant of a range of environmental conditions. This suggests that the gradient along axis 2 is nested within the broader gradient represented by axis 1. Axis 2 scores were negatively correlated at $p \leq 0.001$ with proximity to the stream, shrub cover, animal burrowing and browsing, opening in the conifer canopy over the stream, and valley-floor width, and positively correlated ($p \leq 0.001$) with elevation and distance from the coast (Table 5).

The species groups provide a mechanism for examining general patterns in species–environment relationships. In describing the group patterns below, we integrate results of data analysis with general observations made during fieldwork.

The *Glyceria* group occurred most frequently and with highest percent cover on active floodplains and gravel bars (Table 4; Fig. 4), primarily on wide valley floors in the central and coastal regions of the Coast Range. It was found frequently but with lower cover on back channels, terraces, and alluvial fans. Most of the species in the group seemed to tolerate standing water. Relative to other groups, the *Glyceria* group occurred under the highest percentage of open sky and least amount of deciduous tree and tall-shrub cover (Fig. 5).

The *Petasites* group was most common on gravel bars and floodplains (Table 4; Fig. 4) in the eastern Coast Range. This geographic association was reflected in distance from coast, which was greater than that for all other groups and more than

Fig. 4. Percent cover of species groups across 377 composite sample units. Along the *x* axis, samples are ordered according to the TWINSPAN classification. Vertical lines below the *x* axis indicate predominant sample unit locations as follows: FP, floodplain; GB, gravel bar; HS, hillslope; MS, microsites; TR, terrace; TS, transition slope.



twice that of the *Glyceria* group (Fig. 5). The *Petasites* group generally was found under canopies dominated by deciduous trees; it was associated with the lowest conifer cover of any group (Fig. 5).

The *Urtica* group was found on 8 of 10 gravel bars where cover averaged 1.1% (Table 4; Fig. 4). It occurred less frequently but with higher cover near the stream bank on wet floodplains and terraces. The *Urtica* group was associated with greater mean shrub and deciduous tree cover than the *Glyceria* group (Fig. 5).

Species in the *Chrysosplenium* group were associated primarily with standing water and saturated soils in valley-floor depressions like seeps and remnant back channels (Table 4; Fig. 4), features found most often near the base of hillslopes

Fig. 5. Weighted means of eight environmental variables by species group.

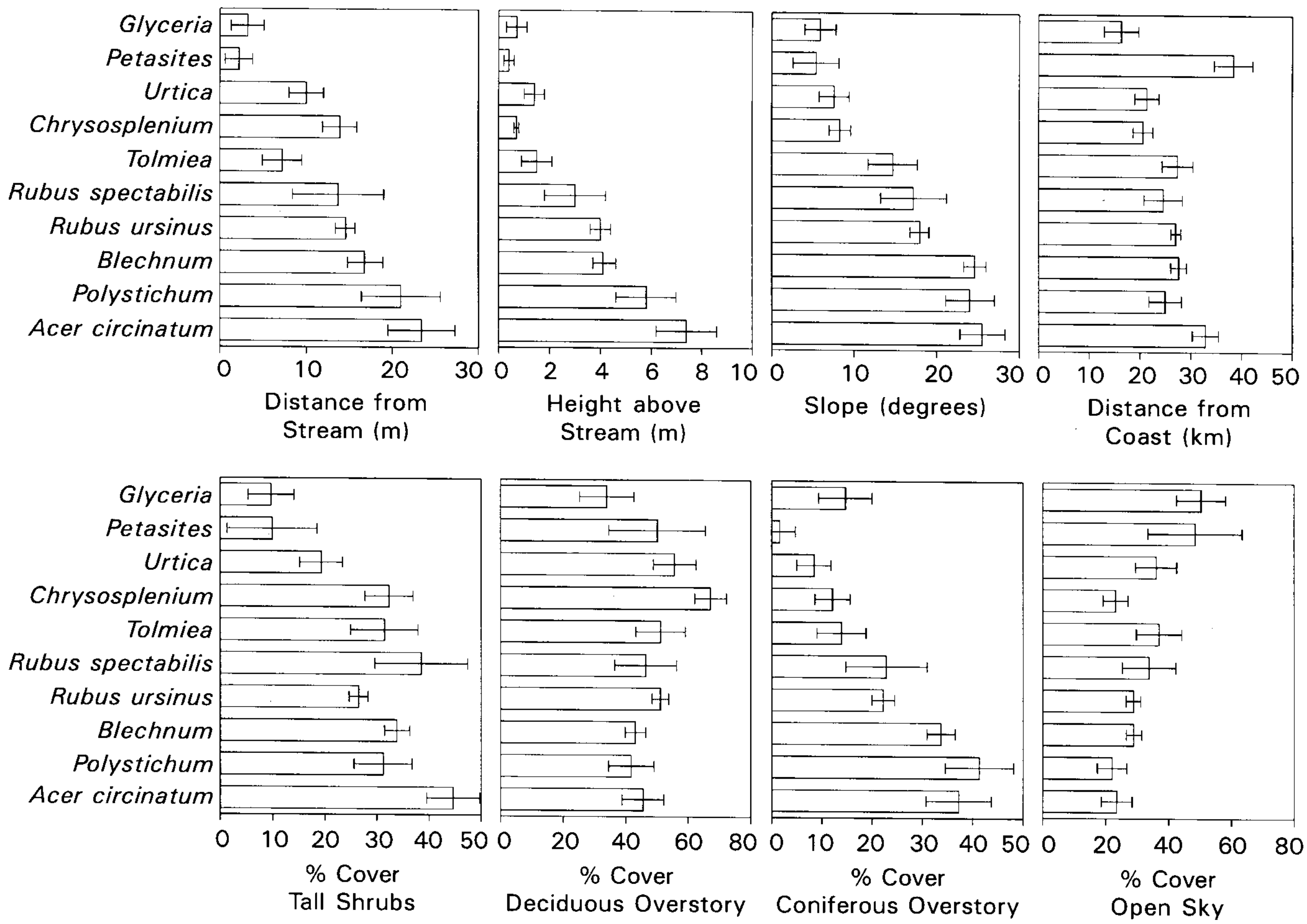


Table 6. Spearman rank correlation coefficients (*r*) between DCA scores and environmental variables for 361 composite sample units with tall shrubs.

Environmental variable	DCA axis 1 (eigenvalue = 0.66)	DCA axis 2 (eigenvalue = 0.51)
Height above stream	0.46	0.35
Distance from stream	0.40	0.26
Percent cover conifer overstory	0.38	0.39
Slope	0.32	0.37
Height of trees on valley floor	0.26	ns
Shrub height	0.24	ns
Percent cover open sky	–0.24	–0.30
Distance from the coast	0.18	0.23
Browsing	ns	–0.26
Height of trees on hillslope	ns	–0.19

Note: Only variables significant at $p \leq 0.001$ for one or both axes are shown. ns, not significant at $p > 0.001$.

on moderately wide valley floors. This topographic position was reflected in the group's values for distance from stream (greater than that for other groups associated with the valley floor) and height above stream (less than that for most other valley-floor groups) (Fig. 5). *Chrysosplenium glechomaefolium* and *Cardamine* spp. (mostly *Cardamine oligosperma* and *Cardamine occidentalis*) also were found near the stream in wet areas and slow-moving water, but *Lysichitum americanum* was restricted to seepy areas (Appendix 1). This group was associated with greater deciduous canopy cover than any other group (Fig. 5).

The *Tolmiea* group was the second most abundant species group (Table 4; Fig. 4), occurring over a wide range of very moist, but not necessarily saturated, soils. It was most promi-

Fig. 6. Scatterplot of DCA scores for tall-shrub species. Directional arrows indicate important environmental gradients identified through correlation analysis.

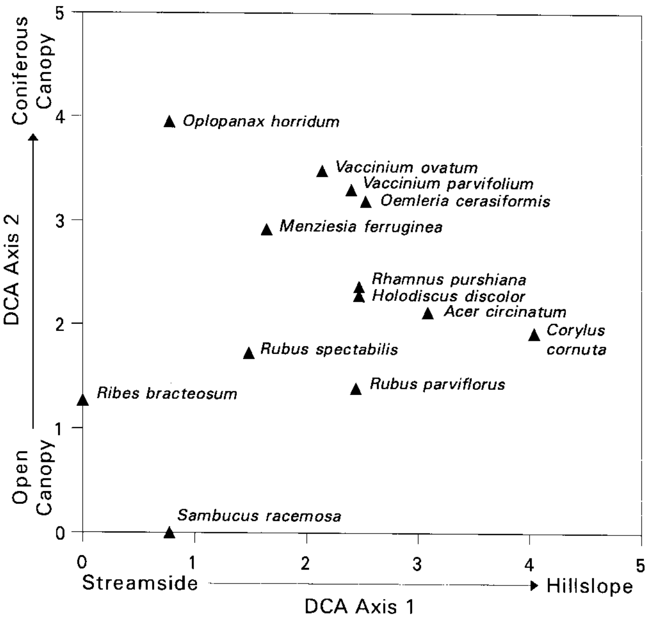


Fig. 7. Species–area relationships by landform, topographic position, or microsite.

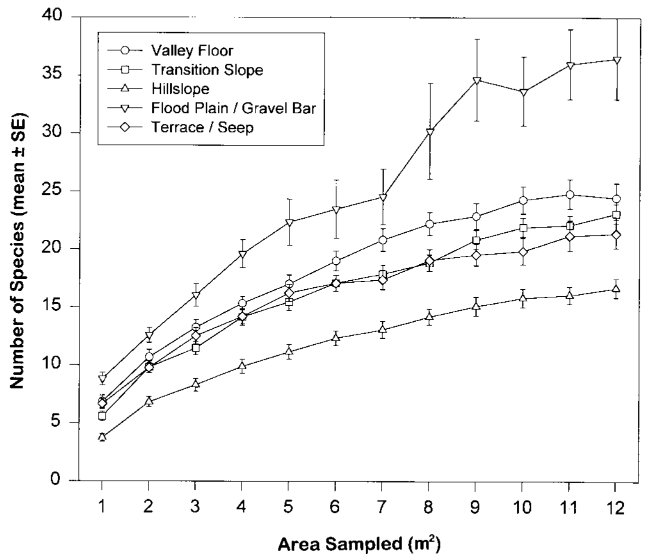
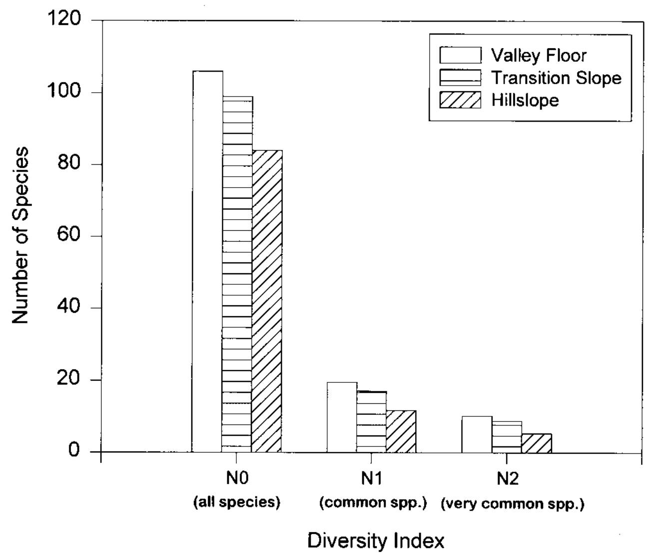


Fig. 8. Species richness and diversity (Hill 1973) on the valley floor, transition slope, and hillslope.



nent on the valley floor. Average cover steadily declined from the floodplain (32.5%) to the lower hillslope (5.8%) (Table 4). On the slope, the *Tolmiea* group was confined mostly to moist areas alongside small drainages.

The *Rubus spectabilis* group was the most abundant assemblage of species in Coast Range riparian areas (Fig. 4). Cover averaged 35.7% overall and the group occurred in all but one composite sample unit (Table 4). Species in this group were found over a broad array of environmental conditions, but were especially dominant on terraces and transition slopes (Table 4). Cover was lower than average on boulders, debris flows, gravel bars, and seeps.

The *Rubus ursinus* group was found in association with recent disturbance on well-drained soils of slopes and high terraces. It averaged 1.3% cover, the least of any group (Table 4). Although members of this group never appeared all together, there were subsets of frequent associates. *Digitalis purpurea* and members of the family Compositae were particularly common on mineral soil exposed near mountain beaver (*Aplondontia rufa*) burrows, found typically at the base of slopes. *Rubus ursinus*, *Pteridium aquilinum*, and *Digitalis purpurea* were associated with openings in young conifer plantations. *Galium aparine* was associated with surface erosion or dry ravel.

The *Blechnum* group was most common on lower hillslopes and transition slopes (Table 4; Fig. 4) on soils that appeared very moist and sometimes unstable or rocky. Three species in this group (*Adiantum pedatum*, *Hydrophyllum tenuipes*, and *Oemleria cerasiformis*) were found chiefly in the eastern Coast Range. *Blechnum spicant*, *Clintonia uniflora*, and *Tiarella trifoliata* grew primarily on woody substrates. *Adiantum pedatum* was found on eroded banks under seepy overhangs.

The *Polystichum* group was widespread on hillslopes and transition slopes, but occurred frequently on terraces and back channels as well (Table 4; Fig. 4). It was much less abundant on floodplains and gravel bars than on hillslopes. On some high terraces under an *Alnus rubra* overstory, *Polystichum munitum* occurred in dense patches interchangeably with *Rubus spectabilis*. *Polystichum munitum* replaced *Rubus spectabilis* as the dominant understory plant under canopies of *Acer macrophyllum*. The shrubs *Vaccinium parvifolium* and *Menziesia ferruginea*, and to a lesser extent *Vaccinium ovatum,* usually were associated with woody substrates (primarily large, rotten conifer logs and snags). The *Polystichum* group was associated with the greatest conifer cover and least open sky of any species group (Fig. 5).

The *Acer circinatum* group occurred on 86% of hillslope sample units with an average cover of 13.1%, and on 64% of transition slope samples, where cover averaged 6.3% (Table 4;

Fig. 4). It was associated with high conifer tree cover and the greatest average shrub cover, slope, distance from stream, and height above stream (Fig. 5).

Tall shrubs

The ordination and gradient analysis of 13 tall-shrub species shows these species arrayed along topographic, canopy-cover, and climatic gradients (Fig. 6). Both axes were positively correlated with height above stream, distance from stream, slope, percent cover of conifers, and distance from the coast, and negatively correlated with percent open sky (Table 6).

Ribes bracteosum, *Oplopanax horridum*, and *Sambucus racemosa* were members of the *Tolmiea* species group described above; however, in the tall-shrub DCA plot they are widely separated along the second axis. *Ribes bracteosum* was common on valley-floor terraces, but was found most frequently on stream banks and transition slopes along constrained stream reaches (Appendix 1). *Oplopanax horridum* occurred in dense patches on terraces, transition slopes, or narrow draws on hillslopes, primarily but not exclusively in the eastern Coast Range. *Oplopanax horridum* occurred frequently with *Ribes bracteosum*, but rarely with *Sambucus racemosa*, which typically was found on wide valley floor terraces under fairly dense deciduous tree cover and in association with *Rubus spectabilis*.

Rubus spectabilis, one of the most abundant and common species in Coast Range riparian forests (Appendix 1), was found colonizing new substrates, occupying forest openings or gaps, and generally growing well under canopies of *Alnus rubra*. It was less abundant under dense canopies of conifers and sometimes *Acer macrophyllum*, as well as on hillslopes and some valley floors in the eastern Coast Range. *Rubus parviflorus* appeared sporadically and in association with *Rubus spectabilis*. Its distribution was limited to recent small disturbances and openings on the slope.

Menziesia ferruginea, *Oemleria cerasiformis*, *Vaccinium ovatum*, and *Vaccinium parvifolium* were found occupying moist hillslope locations, although *Vaccinium ovatum* and *Menziesia ferruginea* also occurred on wide valley floors of conifer-dominated sites near the coast (Appendix 1). All but *Oemleria cerasiformis* occurred frequently on woody substrates. *Acer circinatum*, *Corlyus cornuta* var. *californica*, *Holodiscus discolor* var. *discolor*, and *Rhamnus purshiana* were more common on drier hillslopes at inland locations.

Species–area relationships and species diversity

We encountered a greater number of species per unit area on the valley floor than on the hillslope (Fig. 7). The number of species on the transition slope was intermediate between hillslope and valley floor. A more detailed breakdown of the valley-floor samples revealed that active surfaces (floodplains and gravel bars) supported the most species per unit area, whereas inactive surfaces (terraces and seeps) were comparable with the transition slope (Fig. 7). Standard errors around the means for active surfaces were highly variable beyond 4 m^2 sampling area due to diminished sample size.

Hill's (1973) richness and diversity indices reflect a similar trend (Fig. 8). The valley floor had the greatest values for N0 (total number of species), N1 (common species), and N2 (very common species). The transition slope was intermediate to the valley floor and hillslope.

The streamside to hillslope trend also held true for the proportion of non-native species recorded. On active channel surfaces, 11.4% (9 out of 79) of all species tallied were non-native. For inactive surfaces the proportion was 10.2% (9 of 88), while for transition slopes it was 7.6% (7 of 92) and for hillslopes 4.9% (4 of 82). Some non-native species, including *Prunella vulgaris*, *Digitalis purpurea*, and some Compositae, were found both near the stream and on the slope.

Discussion

General vegetation patterns

This study is the first to provide an extensive description of vegetation–environment patterns and relationships along predominantly narrow streams in the moist, coastal mountains of western North America. We found that vegetation patterns in these riparian forests are highly variable and sometimes indistinct, probably more so than in riparian forests in drier climates, but that vegetation composition is ordered along a complex environmental gradient running from streamside to lower hillslope. Within this trans-riparian gradient, vegetation patterns are further related to specific landforms, topographic positions, microsites, and cover of coniferous tree canopies. The environmental features correlated with these patterns are surrogates for the underlying processes and mechanisms responsible for them. We suggest there are five major drivers of vegetation patterns in riparian forests of the central Coast Range: (*i*) hillslope processes and associated moisture gradients; (*ii*) hydrological disturbance; (*iii*) tolerance of saturated, valley-floor soils; (*iv*) shade tolerance; and (*v*) mineral soil disturbance.

Much of the variation in riparian and lower-slope vegetation of the Coast Range is a product of hillslope processes and the environmental changes associated with ridge-top to valley-bottom gradients. For example, the sequence of species groups *Acer circinatum*, *Polystichum*, *Blechnum*, *Rubus spectabilis*, and *Tolmiea* probably represents a downslope gradient of increasing soil moisture and relative humidity and decreasing moisture stress. Small mesophytic herbaceous species such as those of the *Tolmiea* and *Blechnum* groups may find optimum habitat at the base of these slopes. The length and steepness of the slopes, frequently over 500 m of vertical change in less than 700 m of horizontal distance, coupled with high precipitation (around 200 cm annually), mean that large volumes of water move downslope during the course of the year. Thus, even in this moisture-rich climate, there is an environmental gradient that probably results from the colluvial accumulation of soil water and deeper mineral soils on lower slopes, although changes in these factors with slope position have not been measured in these landscapes. The strength of the gradient may be related to the temporal distribution of precipitation; that is, there is relatively little precipitation during much of the growing season (see Waring and Franklin 1979). Additionally, we observed that changes in vegetation from the valley floor to the lower hillslope (the extent of our sampling) were more dramatic than changes uphill of our sampling, with the exception of dry, exposed ridges or outcrops. This suggests that the moisture gradient is strongest at the base of the slopes. Moisture stress would be further reduced in valley bottoms by fog that is common along the coast in summer. Finally, high rates of soil movement occur where slopes are oversteepened and destabilized by stream downcutting, leading to an accumulation of unstable colluvium at the base of slopes (Kelsey 1988). These locations favor shrub species such as *Rubus spectabilis*, *Ribes bracteosum*, and *Oplopanax horridum*, which appear tolerant of moderate levels of soil disturbance.

The primary driver of “true” riparian vegetation is hydrological disturbance, including periodic floods, erosion, and alluvial deposition. These processes typically operate within a few metres to tens of metres from the actual channel of most Coast Range streams. Species groups showing adaptations to these processes were the *Glyceria* and *Petasites* groups, which were most common on active channel surfaces like gravel bars and floodplains, and the *Urtica* group, which was found on gravel bars, floodplains, and wet terraces. The species in these groups must be able to tolerate soil moisture conditions that range from temporarily saturated to very dry as stream levels fluctuate. They also must have the capacity to withstand the force of peak streamflows or the ability to rapidly colonize bare mineral substrates. The specific autecological characteristics that allow the species in these groups to exist in this environment are virtually unknown. In addition, the actual spatial and temporal soil moisture patterns in floodplains and terraces of these streams have received only limited study (Reiter 1990).

The distribution of other species is related to their tolerance of continuously saturated soils. In particular, species of the *Chrysosplenium* group were found primarily in poorly drained depressions on floodplains and terraces where we observed standing water and saturated soils for significant portions of the year. These conditions were most common in seeps and remnant back channels.

The fourth major factor in the distribution of herbs and shrubs of riparian areas and lower hillslopes appears to be shade tolerance. Gradients of shade occur at two major scales: a stream to hillslope gradient of increasing conifer dominance and understory shade, and an irregular mix of hardwoods, conifers, shrubs, and gaps along the stream. Percent cover of conifers, a measure of the amount of dense shade, was among the strongest correlates with the primary gradient of vegetation composition. Even ubiquitous species such as *Rubus spectabilis* appear to be limited by shade, particularly from conifers. This finding is consistent with Ruth (1970) and Barber (1976). In comparison, deciduous tree canopies allow more light to penetrate in early spring, when many herbs and shrubs have begun growing, and possibly throughout the growing season, although no light measurements have been taken in these forests to substantiate this. This study demonstrates that understories of deciduous hardwood stands are distinct relative to conifer stands. Presumably this is a result of differences in light environments, but other factors such as the moisture and chemical properties of the litter and soil may play an important role (Franklin et al. 1968; Fonda 1974; Van Cleve et al. 1993). Species in the *Glyceria*, *Petasites*, and *Urtica* groups appear to be shade intolerant. These groups were associated with less than 20% cover of tall shrubs and conifers and relatively high amounts of open sky.

Disturbances associated with herbivory, windthrow, unstable soils, logging, and road building also influence species composition throughout the riparian zone and adjacent hillslope. In this study, species of the *Rubus ursinus* group were found most commonly in areas with recently disturbed mineral soils. These species did not appear sensitive to the trans-riparian gradient.

Additional variation in vegetation pattern was introduced by the presence of microsites like seeps, gravel bars, back channels, logs, and boulders. These microsites contribute to variation by providing heterogeneity in substrate and soil moisture conditions. Bendix (1994) also found that factors operating at both transverse (micro) and longitudinal (macro) scales influenced patterns in riparian vegetation. We did not test for variation in multiscale influences, although we did observe regional differences in the distribution of some species or groups. For instance, gravel bars in the more moist parts of the study area were occupied by the *Glyceria* group, but in drier parts they were occupied by the *Petasites* group. Furthermore, distance from the coast (a surrogate for climate) was a significant correlate with the first two axes in the ordinations of all species and tall-shrub species. Additional research is warranted to determine the nature and magnitude of regional-scale variation.

The species groups we describe represent a heuristic device for identifying major patterns in the vegetation and how they relate to landforms and the environment. Species within groups have relatively similar distributions along the environmental gradients, and the presence of several members of a group on a site generally indicates that the habitat conditions common to the group are present. Some groups such as *Chrysosplenium* are comprised of few species with limited distributions, whereas other groups such as *Tolmiea* include numerous species with variable distributions across a range of environmental conditions. Because the groups are comprised of species with individualistic distributions, their application is valid only for the areas we studied. Shifts in habitat relationships and species occurrences are likely as one moves away from the immediate study area.

Tall shrubs

Tall shrubs dominate the understory of these riparian forest communities, probably as a result of the relatively open tree canopies (ranging from 50 to 80% cover), frequent soil disturbance, and moist soil conditions. *Rubus spectabilis* occurred in over 80% of the composite samples, with an average cover of 25.2%. On lower hillslopes, *Acer circinatum* was almost as abundant. Fonda (1974) observed a similar pattern of distribution of these two species in the Hoh River Valley of the Olympic Peninsula. The dominance of tall shrubs in Coast Range forests represents an important biotic control over herb and low-shrub layer composition as well as tree regeneration.

The distribution of *Rubus spectabilis* and other shrub and herb species is compatible with the concept of competitive hierarchies and core habitats (Keddy and MacLellan 1990), in which species are ranked by their competitive abilities for certain productive central habitats. In most forest settings, shade tolerance is the primary factor ordering the competitive abilities of species (Spurr and Barnes 1980). In this riparian – lower hillslope environment, we hypothesize two major organizing factors: (*i*) colonizing ability following disturbance, and (*ii*) shade tolerance. This results in two core habitats: disturbed, productive valley floors with dense canopies of vigorously growing shrubs; and relatively undisturbed, productive hillslopes with dense, conifer canopies. Periodic to frequent disturbance from flooding, debris flows, slope failures, and perhaps high water tables allows *Rubus spectabilis* to colonize and dominate valley floors and many lower slopes. This species invades openings with rapidly spreading rhizomes and germinates on fresh mineral soil; once established, it can perpetuate itself through further cloning, sprouting, and seeding (Tappeiner et al. 1991). In addition, its early phenology allows *Rubus spectabilis* to persist under canopies of *Alnus rubra,* even though it is not very shade tolerant (Barber 1976). These traits enable *Rubus spectabilis* to retard invasion by other plants including trees (Henderson 1978), creating a centrifugal organization of plants around (or in avoidance of) it. For example, *Rubus spectabilis* appears to displace other shrub species to other habitats, including drier (*Rubus parviflorus*), drier and more shaded (*Acer circinatum*), wetter and closer to the stream (*Ribes bracteosum*), and more deciduous tree cover (*Sambucus racemosa*). Other herb and shrub species are displaced to habitats like boulders, logs, gravel bars, active floodplains, saturated soils, and small upland disturbances created by windthrow and herbivory. Carlton (1988) found that diversity of herbs and grasses was lower in the "salmonberry community type" than in other types associated with *Alnus rubra* stands. On the slopes where disturbance is less frequent and soils seem to be well drained, shade-tolerant conifers like *Tsuga heterophylla* and *Thuja occidentalis* organize plant distributions through the dense shade they cast.

Species diversity

Species richness and diversity were higher on the valley floor than on the hillslope, probably reflecting the greater disturbance frequency and environmental diversity of the valley floor. Gregory et al. (1991) and Planty-Tabacchi et al. (1996) also documented higher plant diversity in riparian areas compared with hillslopes in western Oregon and Washington. Within the valley floor, we found that species richness was greatest on open, frequently disturbed floodplains and gravel bars. This suggests that disturbance along these streams is not frequent or severe enough to limit diversity, in keeping with the intermediate disturbance hypothesis (Connell 1978). It is likely that fluvial disturbance and deposition provide new germination sites for a host of highly mobile and shade-intolerant native and non-native species. In addition, the spatial scale of disturbance is uneven, resulting in patches of multi-age vegetation (after Gregory et al. 1991). Nilsson et al. (1989) made a similar observation regarding the spatial distribution of fluvial disturbance and substrate heterogeneity relative to species diversity along riparian corridors in Sweden. However, Baker (1990) found no correlation between spatial variation in disturbance and total species richness along streams in the Colorado Rockies. Additional diversity on the valley floor of Coast Range streams can be attributed to the presence of rotting nurse logs, which provide moist, elevated surfaces where upslope species such as *Vaccinium parvifolium* and *Blechnum spicant* can establish and persist in the presence of a dense shrub layer. Large boulders in the stream channel also afford a unique, elevated environment for herbs such as *Montia parvifolia* and *Mitella ovalis*.

Our finding that the proportion of non-native species was highest where species diversity was highest agrees with the results of Planty-Tabacchi et al. (1996), although the actual proportion that we found in the Coast Range (11.4% on active channel surfaces) was less than half of what they found along larger river systems in Oregon and Washington. They suggest that patch-scale invasibility of riparian communities by non-native species is associated with disturbance frequency, seral stage, and edge-to-area ratio. Hence, it follows that active channel surfaces would have the highest proportion of non-natives. This may have implications at the landscape scale as well, given the high density of streams in the Coast Range. The vast network of relatively open, disturbed streamsides may act as a conduit for the dispersal of non-native species. Our data showing that the proportion of these species was lowest on the slope suggest that the undisturbed hillslope environment may be unsuitable for them. With disturbance, however, upland sites can be colonized by some non-native species.

Conclusions

Vegetation patterns along streams in the deeply dissected mountains of the Oregon Coast Range appear to be associated primarily with hillslope processes and slope-to-stream moisture gradients. Although the distribution of individual species was variable along these gradients, some groups of species occupied distinct locations at the extremes of the gradients (e.g., floodplains and hillslopes) and on some microsites (e.g., seeps). The steep topography in these mountains limits the development and extent of valley-floor landforms, yet this study shows that these surfaces provided hot spots of plant species diversity in what is otherwise a landscape dominated by conifer trees and the herb and shrub species that live beneath them. The distinctness of valley-floor and lower-slope vegetation suggests that riparian zones require a different management and conservation strategy than upland forests. At the same time, the linkage between hillslope and riparian processes, such as water movement and the delivery of large woody debris to the stream, must be recognized in developing such a strategy.

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Appendix 1

Table A1. List of species by species group with frequency of occurrence class and mean percent cover over all sample units and by sample unit location (landforms, topographic positions, and microsites).

	Overall (*n* = 377)		Floodplain (*n* = 45)		Terrace (*n* = 83)		Transition slope (*n* = 94)		Hillslope (*n* = 93)		Alluvial fan (*n* = 3)	
Species group and species	Class	Cover (%)	Class	Cover (%)	Class	Cover (%)	Class	Cover (%)	Class	Cover (%)	Class	Cover (%)
***Glyceria* group**	4	8.5	6	24.7	6	6.0	3	1.7	2	3.0	10	0.8
Agrostis spp.	2	3.2	2	5.2	3	2.8	1	0.5	1	2.0	4	1.1
Dactylis glomerata	1	10.8	1	45.7	1	4.7	1	1.2	1	2.6	—	—
Elymus spp.	1	1.6	2	2.2	1	0.3	1	0.5	1	0.5	—	—
Epilobium watsonii	1	0.7	2	0.9	1	0.6	—	—	1	0.1	—	—
Equisetum arvense	2	2.3	2	2.6	2	0.7	1	0.5	1	0.4	10	0.4
Glyceria spp.	2	3.7	4	7.1	3	1.5	1	0.4	1	0.7	—	—
Oenanthe sarmentosa	2	1.2	4	2.4	4	0.8	2	0.2	1	0.1	4	0.2
Poa spp.	2	4.2	2	7.3	2	4.0	2	2.5	1	5.5	—	
Ranunculus macounii	1	1.6	1	1.2	2	2.4	1	0.8	1	0.4	—	—
Rumex occidentalis	1	0.8	1	1.4	1	0.7	1	0.4	1	0.0	—	—
Scirpus microcarpus	1	10.2	2	26.0	1	2.0	1	0.7	1	0.4	—	—
***Petasites* group**	1	8.0	2	6.2	1	4.3	1	0.4	1	0.1	—	—
Angelica genuflexa	1	3.8	1	2.2	1	0.9	1	0.2	—	—	—	—
Cinna latifolia	1	1.9	1	3.1	1	0.8	—	—	—	—	—	—
Delphinium trolliifolium	1	0.9	1	1.0	1	0.8	1	0.7	—	—	—	—
Petasites frigidus var. *palmatus*	1	9.9	2	6.5	1	5.7	1	0.3	1	0.1	—	—
***Urtica* group**	3	5.0	4	5.0	5	7.2	3	1.5	2	1.3	—	—
Carex obnupta	1	11.6	1	5.2	2	15.1	1	1.7	1	0.6	—	—
Holcus lanatus	1	2.7	1	2.9	1	2.7	1	0.8	1	5.0	—	—
Montia parvifolia	1	0.4	3	0.6	1	0.3	1	0.1	1	0.7	—	—
Nemophila parviflora	1	9.0	1	0.1	1	0.4	1	2.9	1	0.1	—	—
Pastinaca sativa	1	1.8	1	5.6	1	0.2	—	—	—	—	—	—
Prunella vulgaris	1	0.5	1	0.0	1	0.0	1	2.5	1	0.5	—	—
Ranunculus repens	1	3.1	—	—	1	3.7	1	1.9	—	—	—	—
Urtica dioica	2	2.9	2	5.6	3	3.3	1	1.4	1	0.5	—	—
***Chrysoplenium* group**	5	3.0	8	2.9	6	1.2	5	0.8	1	0.1	10	2.2
Cardamine spp.	1	0.3	2	0.3	1	0.2	2	0.1	1	0.1	—	—
Chrysosplenium glechomaefolium	4	2.4	8	2.8	5	0.8	4	0.5	1	0.1	10	2.2
Lysichitum americanum	1	5.3	1	8.0	1	2.4	1	2.2	1	0.0	0	0
***Tolmiea* group**	10	20.4	10	32.5	9	27.8	10	16.9	9	5.8	10	33.0
Athyrium filix-femina	8	5.0	7	8.9	10	5.4	9	3.7	6	1.7	10	2.7
Cardamine angulata	3	0.4	4	0.6	4	0.3	4	0.2	2	0.2	4	7.0
Carex spp.	4	1.2	5	2.0	6	1.4	3	0.9	2	0.8	4	0.2
Circaea alpina	3	0.6	4	0.6	4	0.8	3	0.3	2	0.4	—	—
Corydalis scouleri	1	0.7	1	0.2	1	1.3	1	0.3	1	0.2	4	0.0
Festuca spp.	5	1.3	5	1.9	6	1.3	5	0.8	3	0.7	10	1.4
Mitella caulescens	5	2.4	4	3.1	7	2.8	7	2.1	3	2.2	7	0.3
Mimulus dentatus	6	0.8	7	1.6	7	0.6	6	0.6	4	0.7	10	4.0
Mitella ovalis	4	1.1	4	1.6	5	0.9	4	0.9	2	0.2	10	1.8
Oplopanax horridum	1	11.2	1	18.3	2	8.9	2	11.0	1	5.9	—	—
Osmorhiza chilensis	1	0.3	1	0.5	2	0.3	1	0.2	1	0.2	—	—
Pleuropogon refractus	1	0.8	—	—	1	1.2	1	0.3	—	—	—	—
Ranunculus uncinatus var. *parviflorus*	2	0.3	1	0.6	2	0.2	1	0.2	1	0.1	4	0.5
Ribes bracteosum	5	8.7	5	15.6	6	8.0	5	5.7	3	2.6	10	7.6
Sambucus racemosa	3	4.4	2	3.2	4	4.5	4	3.8	3	3.6	7	2.9
Streptopus amplexifolius	3	0.6	1	0.6	3	1.1	4	0.6	3	0.2	4	0.3
Tolmiea menziesii	8	8.6	10	13.6	10	11.3	9	5.9	4	2.6	10	10.5
Viola glabella	4	0.9	4	0.6	6	0.6	5	0.6	3	0.4	7	0.3
***Rubus spectabilis* group**	10	35.7	10	32.2	10	46.5	10	41.4	10	25.0	10	39.3
Bromus vulgaris	5	2.0	3	2.3	6	1.9	5	2.5	4	1.7	7	0.3
Dicentra formosa	4	0.4	1	0.0	4	0.3	5	0.4	5	0.4	4	0.2

Table A1. (*continued*).

Back channel ($n = 9$)		Boulder ($n = 7$)		Debris flow ($n = 8$)		Eroded bank ($n = 11$)		Gravel bar ($n = 10$)		Log ($n = 4$)		Seep ($n = 10$)	
Class	Cover (%)	Class	Cover (%)	Class	Cover (%)	Class	Cover (%)	Class	Cover (%)	Class	Cover (%)	Class	Cover (%)
7	7.3	2	0.5	2	2.5	1	0.5	7	17.0	3	0.5	6	2.4
2	20.0	—	—	2	2.0	—	—	2	1.5	—	—	—	—
—	—	2	0.5	—	—	—	—	—	—	—		—	—
—	—	—	—	—	—	—	—	4	3.5	—	—	1	6.7
2	1.0	—	—	2	0.5	—	—	2	0.8	—	—	—	—
3	1.5	—	—	—	—	1	0.5	4	13.5	—	—	1	2.0
2	15.0	—	—	—	—	—	—	4	4.9	—	—	2	0.6
5	0.6	—	—	—	—	—	—	6	2.6	—	—	5	0.8
2	0.5	—	—	—	—	—	—	—	—	—	—	2	0.2
—	—	—	—	—	—	—	—	—	—	3	0.5	—	—
—	—	—	—	—	—	—	—	1	1.0	—	—	—	—
3	1.1	—	—	—	—	—	—	1	10.0	—	—	—	—
2	3.5	2	0.5	3	1.1	1	5.3	4	37.2	—	—	1	20.0
—	—	—	—	—	—	—	—	—	—	—	—	1	20.0
—	—	—	—	—	—	—	—	1	0.5	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—
2	3.5	2	0.5	3	1.1	1	5.3	4	37.0	—	—	—	—
3	5.4	3	1.3	—	—	1	2.0	8	1.1	—	—	3	32.0
—	—	—	—	—	—	—	—	—	—	—	—	3	32.2
—	—	—	—	—	—	—	—	1	1.0	—	—	—	—
3	0.4	3	1.3	—	—	—	—	5	0.4	—	—	—	—
2	10.0	—	—	—	—	—	—	1	0.5	—	—	—	—
—	—	—	—	—	—	—	—	1	1.0	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	1	2.0	3	1.4	—	—	1	2.0
9	7.4	3	1.8	3	0.6	2	0.6	6	0.6	3	0.5	9	24.2
4	0.6	—	—	—	—	—	—	2	0.5	—	—	3	0.7
9	3.5	3	1.8	3	0.6	2	0.3	5	0.5	3	0.5	8	19.0
3	15.0	—	—	—	—	1	0.6	—	—	—	—	6	10.7
10	27.5	10	17.4	10	27.4	10	32.1	10	17.5	10	10.3	10	36.4
6	6.8	3	7.7	8	4.0	6	9.5	7	9.8	8	1.8	5	19.1
3	0.5	5	0.7	4	0.8	2	0.2	3	0.7	—	—	2	0.4
3	0.6	3	1.3	5	0.3	3	0.7	4	0.8	—	—	—	—
4	0.6	—	—	2	0.5	1	1.0	3	0.5	3	0.5	—	—
—	—	—	—	—	—	—	—	1	3.3	—	—	—	—
4	2.0	6	5.0	8	0.8	4	0.6	6	1.8	3	5.0	1	1.0
4	3.9	2	5.0	3	0.8	8	2.1	3	0.4	—	—	—	—
9	0.8	8	1.2	9	0.3	2	0.4	7	0.5	3	0.5	1	0.5
4	0.8	8	2.2	7	1.1	1	0.2	3	2.2	5	3.0	2	3.9
—	—	—	—	—	—	1	12.8	—	—	3	5.0	2	37.5
—	—	—	—	2	0.1	—	—	2	1.0	—	—	—	—
—	—	—	—	—	—	1	1.0	—	—	—	—	—	—
2	0.2	3	0.5	2	0.2	1	0.2	1	1.0	—	—	—	—
6	6.1	5	11.7	8	24.7	5	22.4	4	9.6	3	5.0	4	3.6
2	30.0	—	—	—	—	2	3.1	2	0.5	—	—	4	12.0
2	1.0	—	—	3	0.5	3	1.0	1	0.5	3	2.0	—	—
8	17.3	8	4.8	8	4.5	8	12.8	10	2.9	5	5.5	8	8.8
2	0.2	—	—	3	0.3	3	1.0	4	0.4	3	0.5	4	12.7
10	53.8	10	16.0	10	19.5	10	41.8	10	19.6	10	45.5	10	22.3
5	1.8	2	2.0	4	0.4	3	2.6	1	1.0	3	1.0	—	—
—	—	—	—	—	—	5	0.8	—	—	—	—	1	0.2

Table A1. (*continued*).

Species group and species	Overall ($n = 377$)		Floodplain ($n = 45$)		Terrace ($n = 83$)		Transition slope ($n = 94$)		Hillslope ($n = 93$)		Alluvial fan ($n = 3$)	
	Class	Cover (%)	Class	Cover (%)	Class	Cover (%)	Class	Cover (%)	Class	Cover (%)	Class	Cover (%)
Dryopteris austriaca	3	0.9	1	0.3	4	1.5	4	1.1	4	0.4	7	0.6
Galium triflorum	8	0.7	7	0.7	8	0.6	9	0.7	9	0.7	10	0.5
Luzula parviflora	4	0.6	2	0.8	4	0.7	5	0.5	4	0.5	10	0.3
Marah oreganus	2	1.4	1	1.3	1	0.9	2	2.5	2	0.5	4	1.1
Montia siberica	7	0.7	5	0.6	8	0.7	8	0.6	9	0.6	10	1.4
Oxalis oregana	10	10.4	10	12.8	10	12.6	10	9.5	10	8.2	10	15.5
Rubus spectabilis	9	25.2	8	22.0	10	31.0	10	29.6	9	16.9	10	19.8
Stellaria crispa	7	0.4	5	0.3	9	0.5	7	0.4	6	0.3	7	0.6
Stachys mexicana	7	2.1	6	2.8	8	2.7	8	1.8	7	1.6	—	
Trisetum spp.	2	0.9	2	1.2	2	1.1	2	0.7	2	0.6	4	1.2
***Rubus ursinus* group**	5	1.3	4	1.5	6	1.4	5	1.3	6	1.1	7	0.5
Compositae	2	0.3	2	0.6	2	0.2	2	0.3	2	0.1	4	0.4
Digitalis purpurea	1	0.9	1	0.8	1	0.8	2	1.0	2	1.1	—	—
Epilobium spp.	1	0.2	1	0.3	1	0.2	1	0.2	1	0.1	4	0.0
Galium aparine	2	0.7	2	0.9	3	0.7	2	0.7	3	0.6	—	—
Hieracium albiflorum	1	0.1	—	—	1	0.1	1	0.2	1	0.0	—	—
Pteridium aquilinum	1	1.5	—	—	1	1.7	1	1.0	1	1.3	—	—
Rubus parviflorus	1	0.8	1	0.2	1	0.6	2	1.1	2	0.5	4	0.5
Rubus ursinus	2	1.5	1	2.9	2	2.3	2	1.2	3	1.0	—	—
Senecio spp.	1	0.2	—	—	1	0.3	1	0.1	1	0.1	—	—
***Blechnum spicant* group**	8	2.9	6	1.3	8	1.8	9	3.6	8	3.2	7	0.6
Adiantum pedatum	3	1.3	2	1.5	2	1.9	4	1.2	3	0.9	4	0.1
Blechnum spicant	4	2.2	2	2.0	4	1.1	5	2.5	5	2.0	7	0.5
Boykinia elata	1	0.4	1	0.4	1	0.5	1	0.1	1	0.4	—	—
Campanula scouleri	1	0.2	—	—	1	0.2	1	0.2	1	0.1	—	—
Clintonia uniflora	2	0.2	1	0.3	1	0.1	2	0.3	2	0.1	4	0.1
Hydrophyllum tenuipes	3	2.6	2	0.6	3	1.5	4	2.9	3	3.9	—	—
Melica subulata	1	0.9	1	3.0	1	0.7	2	0.5	2	0.6	—	—
Oemleria cerasiformis	1	1.9	1	1.7	1	1.2	2	2.7	2	1.3	—	—
Thalictrum occidentalis	1	0.5	1	0.3	1	0.5	1	0.5	1	0.4	—	—
Tiarella trifoliata	2	0.5	1	0.5	2	0.7	2	0.5	2	0.4	—	—
***Polystichum munitum* group**	9	15.9	5	10.1	10	11.7	10	16.0	10	24.0	10	7.5
Asarum caudatum	1	0.3	—	—	1	0.2	1	0.3	2	0.3	—	—
Disporum hookeri	4	0.5	1	0.9	3	0.4	7	0.5	6	0.4	4	0.5
Maianthemum dilatatum	2	0.7	1	0.3	2	0.6	2	0.6	4	0.7	4	0.2
Menziesia ferruginea	2	1.2	1	1.1	1	0.7	2	1.9	2	1.1	4	0.0
Polystichum munitum	9	15.3	4	12.8	9	11.5	10	14.6	10	21.4	10	7.1
Rhamnus purshiana	1	0.3	1	0.2	1	0.2	1	0.3	2	0.2	—	—
Vaccinium ovatum	1	4.3	1	0.2	1	1.1	1	2.0	1	5.8	—	—
Vaccinium parvifolium	5	1.4	2	0.9	5	1.0	6	1.0	8	2.0	4	0.4
***Acer circinatum* group**	5	9.4	1	29.0	5	4.4	7	6.3	9	13.1	4	0.1
Acer circinatum	4	8.3	1	29.0	4	5.1	4	5.5	7	9.4	—	—
Adenocaulon bicolor	1	0.5	—	—	1	0.5	1	0.4	1	0.6	—	—
Anemone deltoidea	1	0.2	—	—	1	0.1	1	0.2	1	0.2	—	—
Berberis nervosa	1	4.3	—	—	—	—	1	2.8	3	4.7	—	—
Cardamine pulcherrima var. *tenella*	1	0.1	—	—	—	—	1	0.1	2	0.1	4	0.1
Corylus cornuta var. *californica*	1	10.2	—	—	1	7.1	1	14.8	3	8.9	—	—
Gaultheria shallon	2	2.1	—	—	1	0.3	2	1.0	3	3.4	—	—
Holodiscus discolor var. *discolor*	1	1.7	—	—	—	—	1	0.2	1	2.0	—	—
Smilacina stellata	1	2.0	—	—	1	0.1	1	0.6	1	0.9	—	—
Tellima grandiflora	1	0.2	—	—	1	0.4	1	0.2	2	0.2	—	—
Trillium ovatum	2	0.2	—	—	1	0.2	3	0.3	5	0.2	—	—
Vancouveria hexandra	1	0.3	—	—	1	0.1	1	0.2	2	0.4	—	—
Viola sempervirens	1	0.3	—	—	1	0.2	1	0.4	1	0.3	—	—

Note: Frequency classes are as follows (ranges in %): 1, 0–10; 2, 10–20; 3, 20–30; 4, 30–40; 5, 40–50; 6, 50–60; 7, 60–70; 8, 70–80; 9, 80–90; 10, 90–100. *n*, number of sample units.

Table A1. (*concluded*).

Back channel ($n = 9$)		Boulder ($n = 7$)		Debris flow ($n = 8$)		Eroded bank ($n = 11$)		Gravel bar ($n = 10$)		Log ($n = 4$)		Seep ($n = 10$)	
Class	Cover (%)	Class	Cover (%)	Class	Cover (%)	Class	Cover (%)	Class	Cover (%)	Class	Cover (%)	Class	Cover (%)
—	—	—	—	7	0.6	2	0.3	—	—	—	—	2	1.0
5	0.6	6	0.8	9	0.6	5	0.9	8	0.8	3	2.0	1	0.2
—	—	—	—	7	0.4	1	1.6	2	0.5	—	—	—	—
—	—	—	—	2	0.3	1	7.5	—	—	—	—	—	—
4	1.5	3	1.3	4	1.3	5	0.7	4	0.4	5	0.5	5	0.9
9	15.4	9	6.0	9	3.4	7	6.1	10	8.6	10	22.8	8	10.2
10	37.6	5	21.7	9	16.2	9	41.0	9	8.6	8	28.3	9	13.7
6	0.5	6	0.6	7	0.5	6	0.7	4	0.5	3	2.0	4	0.6
8	0.9	2	0.5	3	0.2	5	3.0	4	4.4	—	—	3	2.8
—	—	2	0.5	3	0.6	—	—	2	1.6	—	—	—	—
4	1.4	—	—	4	1.2	4	0.8	3	1.8	—	—	1	0.5
2	0.5	—	—	2	2.0	1	0.1	2	0.5	—	—	1	0.5
2	0.2	—	—	—	—	1	0.3	2	0.5	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	2	0.5	3	0.9	1	0.5	—	—	—	—
2	0.5	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	2	1.3	—	—	—	—
2	3.0	—	—	3	0.5	1	0.2	1	0.5	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—
4	1.8	2	0.5	7	2.1	7	5.5	3	2.3	5	15.5	4	3.5
—	—	—	—	3	0.2	3	3.4	1	6.0	—	—	—	—
2	2.0	2	0.5	3	4.1	1	2.1	—	—	5	15.0	2	4.6
—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	1	0.5	—	—	—	—
—	—	—	—	3	0.1	1	0.0	—	—	3	0.5	—	—
2	3.0	—	—	—	—	4	3.1	1	0.5	—	—	1	4.0
2	0.2	—	—	2	1.3	3	2.9	—	—	—	—	—	—
—	—	—	—	—	—	1	5.0	—	—	—	—	1	0.5
—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	3	0.5	1	0.2
8	10.0	5	22.0	10	4.0	6	4.9	4	4.2	10	3.0	5	10.1
—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	2	0.1	3	1.6	—	—	5	2.7	—	—
—	—	—	—	2	1.2	1	2.5	—	—	—	—	1	0.2
—	—	—	—	2	0.2	—	—	1	0.5	—	—	1	0.5
7	11.6	5	21.8	9	3.6	4	5.6	2	6.9	—	—	4	8.5
—	—	—	—	2	0.2	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	1	15.0
2	0.5	2	0.5	7	0.9	—	—	2	1.3	8	2.2	2	0.4
2	14.8	—	—	4	0.7	5	15.3	—	—	3	20.5	1	4.0
—	—	—	—	—	—	4	18.9	—	—	3	20.0	1	4.0
—	—	—	—	—	—	—	—	—	—	3	0.5	—	—
—	—	—	—	2	1.3	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	3	0.3	—	—	—	—	—		—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—
2	14.8	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	2	0.1	2	0.3	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—	—	—