Structure and composition of unmanaged riparian forests in the coastal mountains of Oregon, U.S.A.[1]

Robert J. Pabst and Thomas A. Spies

Abstract: We characterized the structure and composition of unmanaged riparian forests in three river basins in Oregon's coastal mountains. Our objective was to evaluate stand attributes at three spatial scales: streamside (site), drainage network (stream order), and basin (subregion). Data on basal area, species composition, snag density, canopy cover, and tree regeneration were collected along transects at 124 sites. Conifer basal area increased with distance from stream, a trend similar among subregions, and was highest at sites along first-order streams. Hardwood basal area was relatively constant with distance from stream and was proportionally higher at sites along second- and third-order streams than at sites along first-order streams. Conifer and hardwood tree regeneration occurred infrequently and varied by topographic position, stream order, and subregion. Conifer regeneration was associated with basal area of shade-tolerant conifers and appeared to be limited by shrub competition. The unmanaged forests we studied were characterized by a patchy mosaic of structure and composition. Hardwoods and shrubs were major components of the near-stream environment in these forests, whereas dominance of conifers was limited to hillslopes. It appears that fine-scale patterns associated with proximity to the stream are influenced by coarser scale factors such as valley-floor width and climate.

Résumé : Les auteurs ont caractérisé la structure et la composition des forêts riveraines non aménagées dans les bassins de trois rivières des montagnes côtières de l'Oregon. Leur objectif était d'évaluer les attributs du peuplement à trois échelles spatiales : celle du bord du cours d'eau (site), celle du réseau de drainage (ordre du cours d'eau) et celle du bassin (sous-région). Les données concernant la surface terrière, la composition en espèces, la densité des chicots, le recouvrement de la canopée et la régénération des arbres ont été récoltées le long de transects, dans 124 sites. La surface terrière des conifères augmente de façon similaire entre les sous-régions avec la distance par rapport au cours d'eau. Son maximum est atteint sur les sites situés le long des cours d'eau du premier ordre. La surface terrière des feuillus demeure relativement constante avec la distance par rapport au cours d'eau. Elle est proportionnellement plus élevée sur les sites qui longent les cours d'eau des deuxième et troisième ordres que sur ceux situés le long des cours d'eau du premier ordre. La régénération des arbres conifériens et feuillus n'est pas fréquente et varie avec la position topographique, l'ordre du cours d'eau et la sous-région. La régénération des conifères est associée à la surface terrière des conifères sciaphiles et semble être limitée par la concurrence des arbustes. Les forêts non aménagées étudiées sont caractérisées par une mosaïque inégale de structure et de composition. Dans ces forêts, les feuillus et les arbustes représentent les composantes majeures de l'environnement proche du cours d'eau, alors que la dominance des conifères est limitée aux versants des collines. Il semble qu'à plus petite échelle les patrons associés à la proximité des cours d'eau soient influencés par des facteurs qui interviennent à plus grande échelle tels que la largeur du fond de la vallée et le climat.

[Traduit par la Rédaction]

Introduction

Riparian forests are at the focal point of issues on biodiversity and forest management in the Pacific Northwest and elsewhere. Central to these issues is the need for basic ecological information about the structure, dynamics, and function of riparian forests that could be useful for designing conservation and management strategies. For example, how do the structure and composition of unmanaged riparian forests relate to landform, stream order, and disturbance history? Are there predictable patterns in the distribution of tree species in unmanaged forests that could be imitated in managed forests? Understanding such patterns and relationships is particularly challenging in riparian areas because they are subject to spatially complex, multiscale processes. The vegetation along any one reach of stream may be cumulatively influenced by factors operating at scales measured from metres (e.g., proximity to the stream), to tens or hundreds of metres (e.g., valley morphology), to hundreds or thousands of metres (e.g., location in the drainage network). Furthermore, regional variation in climate, geology, and disturbance history may affect spatial relationships at finer scales,

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R.J. Pabst.[2] Department of Forest Science, College of Forestry, Oregon State University, Corvallis, OR 97331, U.S.A.
T.A. Spies. Pacific Northwest Research Station, USDA Forest Service, 3200 Jefferson Way, Corvallis, OR 97331, U.S.A.

[1] Paper No. 3321 of the Forest Research Laboratory, Oregon State University, Corvallis.

[2] Corresponding author. e-mail: rob.pabst@orst.edu

making it difficult to extrapolate the results of stand or stream-reach studies in one drainage basin to conditions throughout the basin or in other basins.

Our understanding of riparian forest patterns comes mostly from studies that examined how vegetation varies at the scale of stream reaches, that is, from the stream toward the uplands. Findings from numerous geographic locations associate the distribution of tree species with distinct alluvial landforms, lateral zones of flood disturbance, and various environmental factors that change with distance from the stream. The underlying mechanisms found or hypothesized to control vegetation patterns include soil moisture and depth to water table (Hawk and Zobel 1974; Frye and Quinn 1979), soil texture and size of coarse fragments (McBride and Strahan 1984), soil pH (Sagers and Lyon 1997), successional status (Fonda 1974), and the severity (Osterkamp and Hupp 1984; Bendix 1994) and frequency (Bell 1974; Irvine and West 1979; Harris 1987; Cordes et al. 1997; Nakamura et al. 1997) of flooding. The focus of these studies was on valley-bottom forests, while a few others have also incorporated the lower hillslope (Hack and Goodlett 1960; Andrus and Froehlich 1988).

Less well known is how riparian vegetation patterns are influenced by factors operating at broader spatial scales, such as location in the stream network or across regional climatic gradients. Hupp (1986) surveyed the distribution of woody species across a range of stream orders in Virginia. He concluded that channel gradient controlled the processes that form channel shelves and floodplains, which in turn determined species distributions. Species associated with floodplains of lower gradient, higher order streams were generally absent along higher gradient, lower order streams where floodplain development was limited or nonexistent (Hupp 1986). Baker (1989) and Bendix (1994) assessed the relative importance of factors operating at different spatial scales. In the southern Rocky Mountains, Baker (1989) found that regional (“macroscale”) factors such as drainage basin area and elevation were more important in controlling vegetation patterns in some riparian environments, while local (“microscale”) factors such as valley morphology were more important in others. These results signify spatial variability in the influence of ecological processes. Bendix (1994) found that woody vegetation patterns along streams in the coastal mountains of southern California resulted from the combined influence of factors operating within sites (height above water table, flood severity, substrate texture) and between sites (valley width and orientation, elevation, fire history). No studies have explicitly addressed scale issues in riparian forests of the Pacific Northwest.

Our interest was to understand how the structure and composition of unmanaged riparian forests in the coastal mountains of Oregon varied at three spatial scales: by proximity to the stream (site), among locations in the drainage network (stream order), and across regional climatic and geologic gradients (subregion). In addition, we wanted to know if there were interactions among these dimensions of environmental variation. Our research objectives were driven by the need for baseline information on unmanaged riparian forests in a landscape dominated by intensively managed forests. Such information is important to land managers and policy makers in the Pacific Northwest who are attempting to develop watershed- and regional-scale plans to maintain or restore high-quality habitat for threatened stocks of anadromous salmonids (Forest Ecosystem Management Assessment Team (FEMAT) 1993; Hayes et al. 1996; Nicholas 1997). High-quality fish habitat in this region frequently is associated with large, coniferous, woody debris, which provides refuge and habitat complexity for the fish (Bisson et al. 1987). Consequently, riparian forest practices laws and management policies emphasize retaining conifer trees in streamside buffer strips or establishing and growing conifers where they are lacking (FEMAT 1993; Oregon Department of Forestry 1994). However, without basic data on the structure, composition, and spatial distribution of trees in unmanaged riparian forests, it may be difficult to develop and evaluate silvicultural practices to meet aquatic conservation goals.

Until recently (McGarigal and McComb 1992; Minore and Weatherly 1994; Hibbs and Giordano 1996; Pabst and Spies 1998; Nierenberg and Hibbs, in press), very little information had been published on the structure and composition of riparian forests in unmanaged settings in the coastal mountains of Oregon. Still lacking are studies of how stand features vary across spatial scales. There is particular interest in the distribution of conifer tree regeneration. Therefore, our objectives were to (*i*) characterize the structure and composition of the live and dead tree canopy layers in unmanaged riparian forests in relation to distance from stream and topographic position; (*ii*) characterize patterns of tree regeneration in relation to substrate, canopy characteristics, and topographic position; and (*iii*) evaluate how site-level patterns in stand attributes vary at coarser spatial scales, namely stream orders and subregions.

Methods

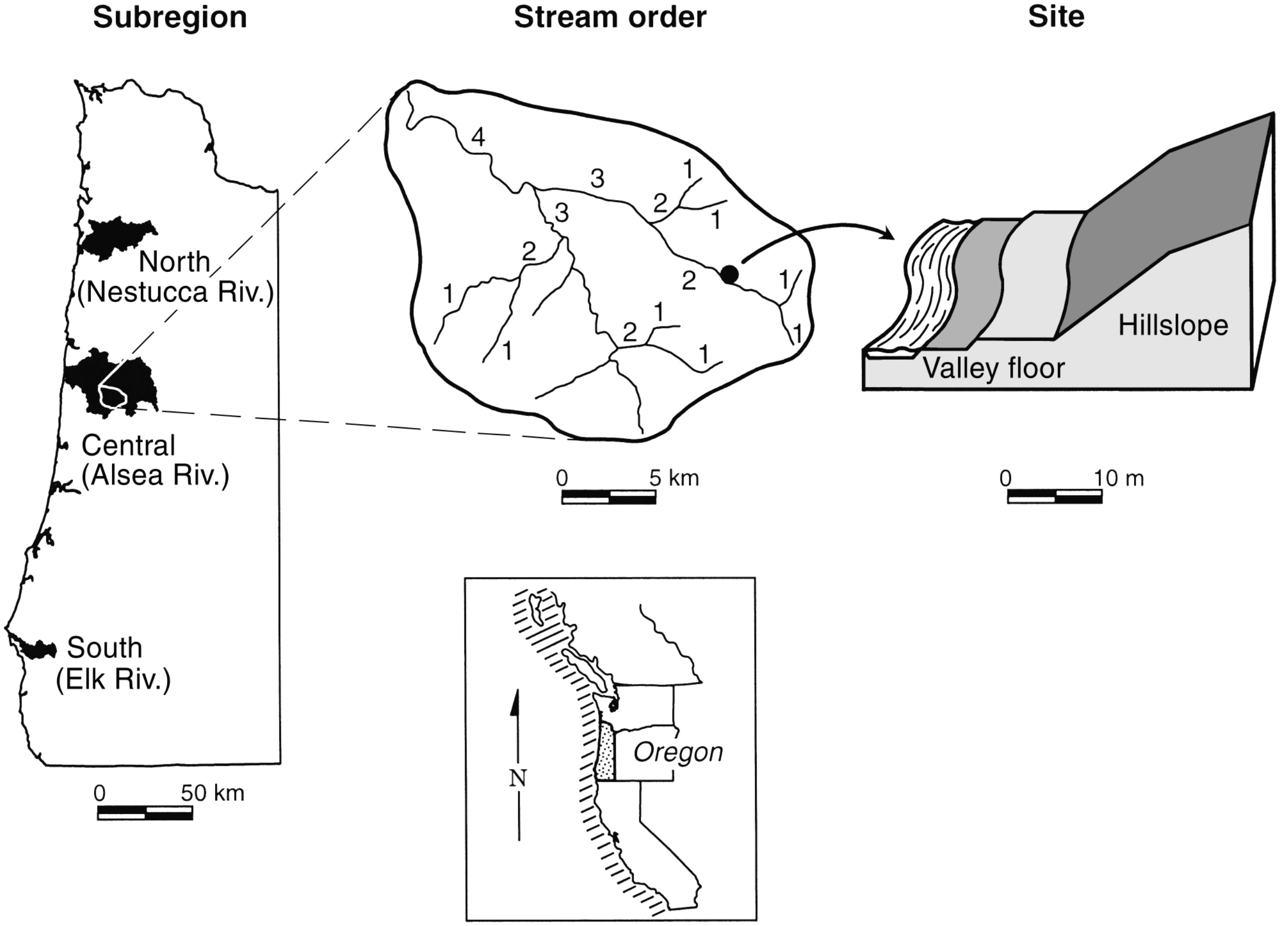
Study area

The study area included three subregions in the coastal mountains of Oregon: (*i*) north (Nestucca River basin, Coast Range); (*ii*) central (Alsea River basin, Coast Range); and (*iii*) south (Elk River basin, Klamath Mountains) (Fig. 1). The Coast Range physiographic province is underlain by substrata of uplifted ocean floor sediment and basalt flows from the Tertiary period (Miocene and Eocene epochs) (Franklin and Dyrness 1973). The Klamath Mountains physiographic province is comprised of older, more complex formations of uplifted and folded ocean floor sediment and granitic intrusions from the Cretaceous and Jurassic periods (McHugh 1987). The terrain is steep and rugged. Elevations in the study area range from near sea level to about 1250 m, but most ridgetops are less than 700 m.

Climate of the study area is strongly influenced by the Pacific Ocean, with plentiful precipitation that occurs mostly as rain from October through May. Average annual precipitation ranges from 150 to 350 cm (Ruffner 1985). Summers are usually mild to warm and dry, with lingering fog in a narrow belt along the coast that can contribute to precipitation in the form of fog drip (Azevedo and Morgan 1974). Temperatures across the three subregions are similar, although differences between mean maxima and minima during summer are greater with distance from the ocean and from north to south in the study area (Taylor 1993).

All three subregions are deeply dissected by a dense network of perennial and intermittent stream channels. Streamflow regimes closely track precipitation patterns, with peak flows in winter and low flows in late summer or early autumn. Drainage basin area varies substantially among the three primary basins, with the Alsea

Fig. 1. Location of north, central, and south subregions in the coastal mountains of Oregon and a representation of the spatial scales at which stand attributes were compared.



(central) being the largest at about 121 000 ha, followed by the Nestucca (north) at about 66 000 ha (excluding the Little Nestucca River), and the Elk (south) at about 23 500 ha.

The north and central subregions include two vegetation zones: the Sitka spruce (*Picea sitchensis* (Bong.) Carr.) zone, which coincides with the coastal fog belt, and the western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) zone, which dominates the interior (Franklin and Dyrness 1973). The south subregion is wholly in the western hemlock zone but is influenced and bordered on the east and south by the mixed evergreen zone (Franklin and Dyrness 1973). In each subregion, clearcut logging has been extensive, resulting in a patchwork of managed and unmanaged forest stands. Each subregion also has roadless areas or wilderness areas comprised of unmanaged forest. Ownership is mixed public and private, although most of the unmanaged forest is on public land, where we conducted our sampling.

Existing unmanaged forests developed primarily after large, stand-replacing fires; there is evidence that these fires burned through riparian areas (Poage 1994). The most recent fire of this magnitude in the north subregion was in 1902 (Morris 1934). Unmanaged stands in the central subregion established after fires in the mid-1800s and are mostly 130–150 years old (Morris 1934; Poage 1994), although there are scattered locations with unmanaged younger (60–80 years) and old-growth (>200 years) forest. Fire disturbance in the south subregion may have been more frequent and patchy (Agee 1991). At many sites in the south subregion the oldest trees were about 80 years of age, but several sites had remnant old-growth trees. Other natural disturbances such as wind storms, landslides, flooding, and pathogens have played an important role in coastal forest dynamics but usually at smaller scales than the large fires.

Study sites

A study site was defined as the area from the stream to the lower hillslope along one side of a 100-m reach of stream. We selected sites subjectively from aerial photographs and field reconnaissance to sample a range of geographic locations, stream orders (Horton 1945) (first through third order in the north and south subregions, first through fifth order in the central subregion, as determined from 1 : 24 000 topographic maps), valley-floor widths, and tree canopy types (conifer-dominated, hardwood-dominated, mixed). Patches of tree canopies appearing to be relatively uniform on aerial photographs were sometimes quite variable on the ground. In addition, most sites contained treeless, shrub-dominated gaps ranging in size from a few square meters to thousands of square metres. Both sides of the stream were sampled along most reaches, but these were treated as separate sites because of differences in landform configuration, aspect, and, frequently, vegetation characteristics (Minore and Weatherly 1994; Pabst and Spies 1998). There were 17 sites along 10 streams in the north subregion, 75 sites along 34 streams in the central subregion, and 32 sites along 11 streams in the south subregion (Table 1).

All sites were located in unmanaged forest, meaning there was no evidence of past tree harvest or obvious and extensive human occupation. Stands at these sites were in relatively mature stages of development, with ages of most hillslope conifers dating to the fires that occurred 80 or more years ago. On valley floors, tree

Fig. 2. Data collection scheme (basal area data collected at fixed points (●); tree regeneration and canopy cover data collected in 4 × 4 m plots; snag data collected in 16 × 16 m plots).

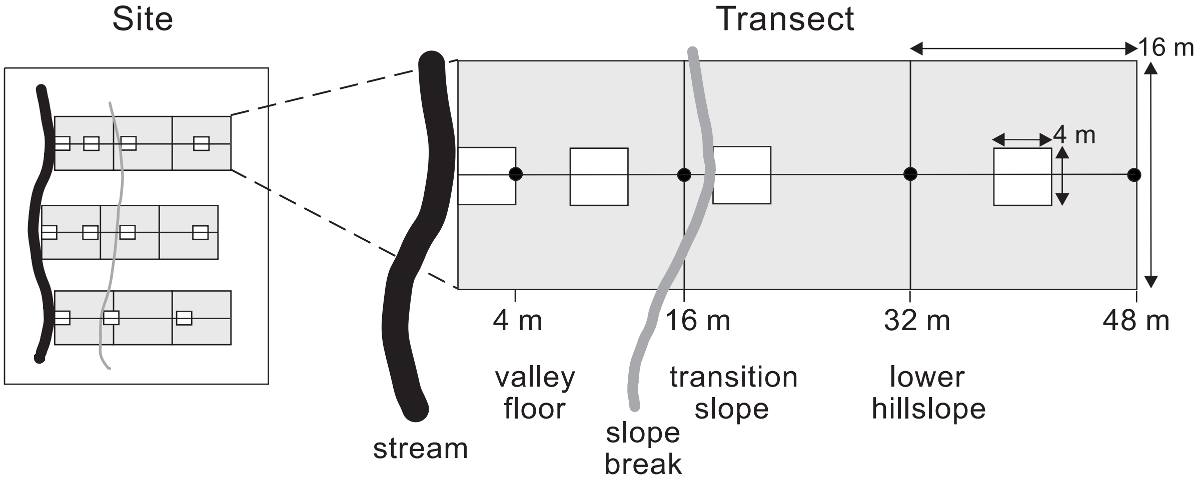


Table 1. Number of sites (*n*) and means (with ranges given in parentheses) of study site characteristics by subregion and stream order.

Subregion	Stream order	*n*	Bankfull width of stream (m)	Valley-floor width (m)	Stream gradient (degrees)	Elevation (m)	Distance from coast (km)
North	First	5	4.4 (3.3–5.7)	13.6 (11.9–16.1)	5.7 (1.7–7.7)	317.3 (244–463)	16.5 (3.2–32.2)
	Second	6	5.9 (3.7–8.7)	16.1 (5.8–22.0)	5.8 (4.0–8.7)	324.3 (232–375)	17.1 (15.3–18.5)
	Third	6	10.6 (9.2–12.5)	42.1 (30.3–48.7)	2.4 (1.5–3.3)	211.0 (177–262)	26.7 (23.7–29.8)
Central	First	14	2.8 (0.7–4.6)	11.7 (0.7–49.3)	12.6 (4.0–23.7)	330.0 (134–610)	26.9 (4.8–46.7)
	Second	30	4.2 (2.0–6.9)	27.9 (5.3–83.7)	4.0 (1.7–8.3)	184.2 (49–329)	27.4 (10.7–44.8)
	Third	23	8.6 (5.2–14.3)	40.8 (6.5–95.6)	2.9 (1.0–8.3)	167.2 (37–330)	21.2 (1.6–43.5)
	Fourth + fifth	8	21.1 (9.6–32.7)	85.3 (20.4–135.4)	1.3 (0.7–2.0)	141.8 (49–293)	23.1 (8.0–38.1)
South	First	8	6.1 (5.6–6.5)	11.1 (6.4–21.7)	4.6 (3.7–6.7)	399.0 (182–597)	19.3 (12.9–29.0)
	Second	8	8.1 (5.7–9.4)	19.4 (5.7–36.9)	3.8 (1.7–7.0)	218.8 (85–500)	15.1 (8.0–25.7)
	Third	16	14.9 (9.2–19.8)	50.9 (11.4–117.8)	2.0 (1.0–4.3)	221.9 (18–378)	16.9 (5.6–22.5)

ages at some sites reflected more recent fluvial disturbances. Some of the sites in each subregion (2 in the north, 20 in the central, 16 in the south) were in wilderness areas, research natural areas, or municipal watersheds. The rest were in remnant forest patches ranging in size from 20 to hundreds of hectares; these patches often were close to (0.2 to 1 km from) forest plantations, clearcut harvest units, or logging roads.

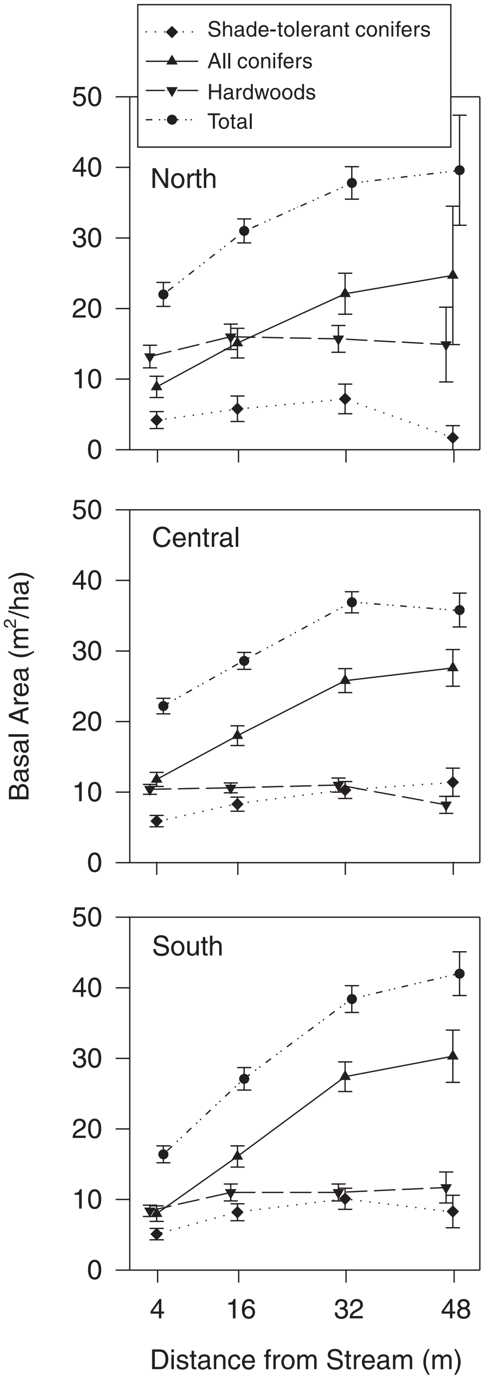
Data collection

Data were collected from 1989 to 1992. At each site, we recorded data at fixed points and in plots along two or three transects that extended from the stream edge to about 32 m up the lower hillslope in a direction roughly perpendicular to streamflow (Fig. 2). Total transect length and the number of points and plots along the transect depended on width of the valley floor. For example, along constrained stream reaches where the hillslope essentially began at the stream's edge, transects were just 32 m long; at sites with valley floors, transect lengths ranged from 33 to 112 m. The location of the first transect was chosen randomly within the upstream section of the study reach. Successive transects were 25 m apart in a downstream direction.

Basal area of live trees was estimated using a wedge prism (4.6 or 9.2 m^2/ha basal area factor, depending on average stand diameter) at fixed distances from the stream along each transect: at 4 m, 16 m, and every 16 m beyond that to the end of the transect (Fig. 2). One drawback to using a prism was the potential for tallying the same tree from one sample point to the next along a transect. This would most likely occur with large diameter trees, and might obscure differences in basal area between sample points. Conifer and hardwood snags were counted in 16 × 16 m plots that were contiguous along the transects. Minimum snag size was 2 m tall and 25 cm diameter at breast height (DBH). In the north and south subregions, we also noted the topographic position (valley floor or hillslope) on which each live tree or snag occurred. This modification to the data collection protocol was done after our work in the central subregion.

Data also were collected in 4 × 4 m plots. Tree regeneration, represented by counts of seedlings more than 1 year old, saplings, and small trees up to 15 cm DBH, was recorded by species and rooting substrate. Cover of conifer trees, deciduous hardwoods, evergreen hardwoods (south subregion only), tall shrubs (>1.5 m), and open sky (all measured independently so their sum could exceed 100%) were measured from the center of each plot with an optical canopy viewer (Mueller-Dombois and Ellenberg 1974). We also estimated cover of logs (exposed surfaces only), moss, and bare ground. Finally, we measured slope, aspect, distance from stream, and height above stream for each plot. The 4 × 4 m plots were located on 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). Additional valley-floor sampling was done along streams with valley floors wide enough to accommodate more than a single plot. There were at least 2 and up to 10 plots per transect, and from

Fig. 3. Basal area by subregion and species type (shade-tolerant conifers, all conifers (shade-tolerant species + Douglas-fir), and hardwoods).



5 to 29 plots per site, depending on the width of the valley floor. There were 144 plots in the north subregion, 954 in the central subregion, and 300 in the south subregion, for a total of 1398 plots.

We also characterized the physical environment at transects and sites (Table 1). For each transect, we recorded valley-floor width, bankfull stream width, stream gradient, and area of the hardwood and conifer canopy gaps over the stream. Gap area (degrees squared) was estimated by measuring from zenith the angles at which sight lines were intersected by the canopy in directions perpendicular and parallel to the stream course. For each site, we recorded stream order, elevation, distance from the coast, and the height and age of representative trees on the valley floor (if present) and hillslope.

Data analysis

Basal area, tree species composition, snag density, canopy cover, and tree regeneration were compared with descriptive statistics at three spatial scales: site, stream order, and subregion. The site scale was represented by topographic position (valley floor, transition slope, lower hillslope) or distance from stream. Data from beyond 48 m were not included in the distance-based summaries. Data from fourth- and fifth-order streams in the central subregion were combined because of small sample sizes. In addition, we combined the three size classes of tree regeneration into a single class because of a general lack of regeneration.

Tree regeneration data were analyzed in more depth. Species composition was calculated as the percentage of 4 × 4 m plots in which each regenerating species was present, rather than a percentage of the total number of regenerating trees, to minimize the influence of plots containing unusually large numbers of seedlings. Classification and regression tree (CART) analysis (Breiman et al. 1984; Clark and Pregibon 1992; Mathsoft, Inc. 1997) was used to identify factors important in determining the presence or absence of conifer tree regeneration in a plot. CART analysis was chosen over logistic regression because it effectively handles different variable types and non-normal data, and it can elucidate interactions among variables (Michaelsen et al. 1994; Hansen et al. 1996). Predictor variables included subregion, stream order, and other continuous and categorical data collected at the site, transect, and plot levels. Plots were assigned basal area values from the basal-area measuring point nearest the plot.

Results

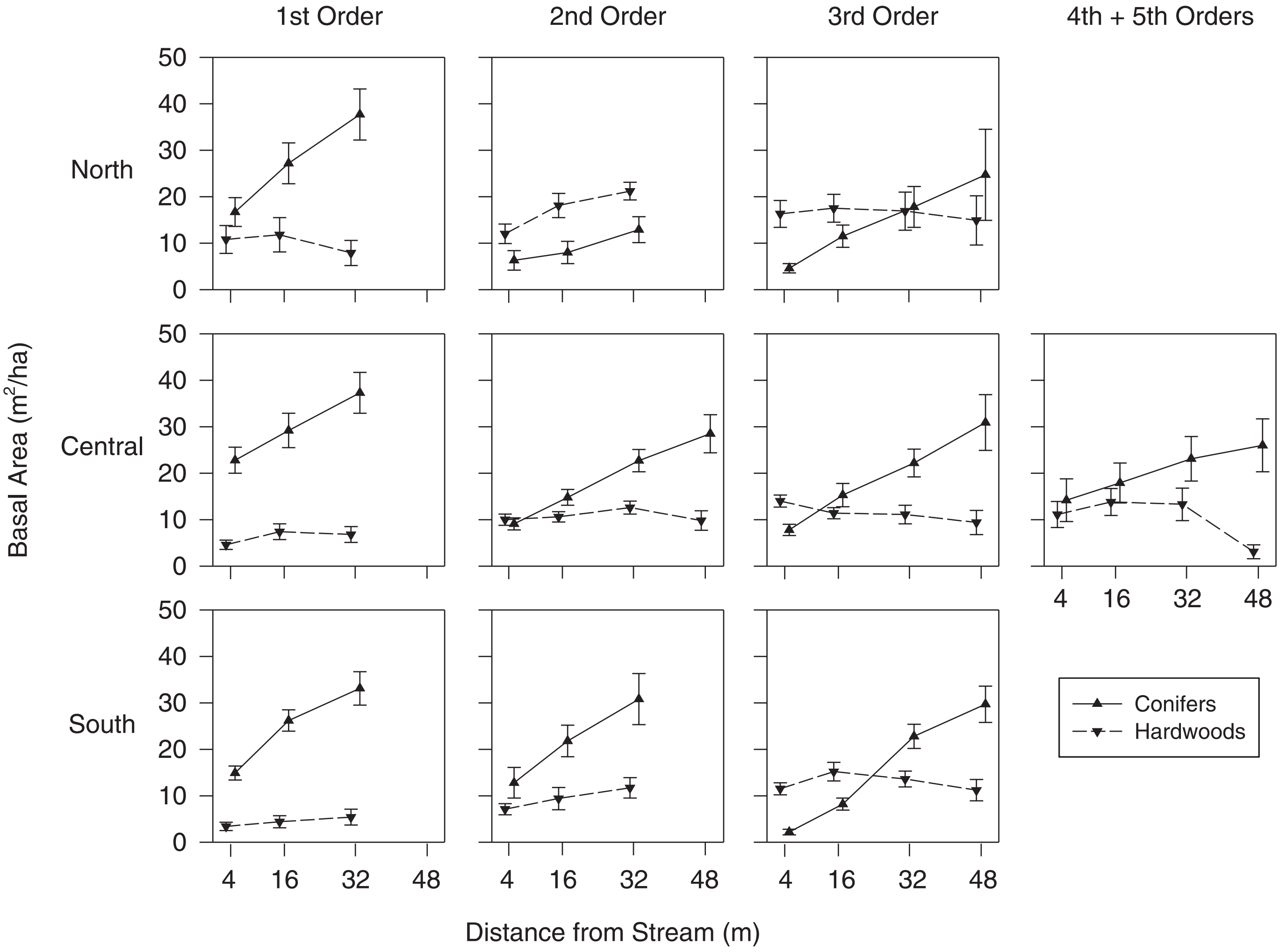
Basal area of live trees

Average basal area of conifer trees increased with distance from the stream in all three subregions, whereas that of hardwood trees was relatively constant (Fig. 3). Basal area of shade-tolerant conifers (western hemlock, western redcedar (*Thuja plicata* Donn), and either Sitka spruce (north, central) or Port-Orford cedar (*Chamaecyparis lawsoniana* Parl.) (south)) was 4–10 m^2/ha within 32 m of the stream in each subregion and increased with distance at a slower rate than basal area of all conifers (shade-tolerant species plus Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco)) (Fig. 3).

Other trends in basal area were evident at the stream-order scale. In the north and central subregions, conifer basal area at sites along first-order streams was greater than at sites along all other stream orders at all distances (Fig. 4). In the south subregion, conifer basal area was similar at sites along first- and second-order streams and greater than that at sites along third-order streams. Hardwood basal area generally was least along first-order streams; it was greater than conifer basal area at 4 m from third-order streams in all subregions (Fig. 4).

Species composition of the basal area tallies varied with distance from stream, stream order, and subregion. In the north subregion, red alder (*Alnus rubra* Bong.) and Douglas-fir comprised the majority of basal area tallies. Red alder was dominant at 4 and 16 m from the stream for each stream order (Table 2). In the central subregion, Douglas-fir was the dominant species along first-order streams at 4 m and beyond, along second-order streams at 16 m and beyond, and along third- through fifth-order streams at 32 and 48 m (Table 2). Red alder ranked highest in basal area at distances

Fig. 4. Basal area by subregion, stream order, and species type (conifers, hardwoods).



not dominated by Douglas-fir. Sitka spruce was prominent at sites along fourth- and fifth-order streams; it was not found more than 20 km from the ocean. In the south subregion, western hemlock comprised at least 30% of the basal area at 4 and 16 m along first- and second-order streams, while Douglas-fir was dominant at 32 m for each stream order (Table 2). California laurel (*Umbellularia californica* (H. & A.) Nutt.) and bigleaf maple (*Acer macrophyllum* Pursh) were major components of basal area at sites along second- and third-order streams in the south subregion.

Species composition of basal area was also related to topographic position. In the north subregion, red alder was the most frequently tallied species on active floodplains and terraces, in contrast to hillslopes where the percentage of red alder and Douglas-fir was about the same (Table 3). In the south subregion, red alder was the dominant floodplain tree; red alder, bigleaf maple, and Douglas-fir were prominent on terraces; and Douglas-fir dominated hillslopes (Table 3). Data on basal area by topographic position were not collected in the central subregion.

Density of snags

The average density of conifer snags increased with distance from the stream in all three subregions, except along third- through fifth-order streams in the central subregion (Table 4). Conifer snag density was highest at sites along second-order streams in the north subregion, highest along first-order streams in the central subregion, and showed no clear trend in the south subregion. Most of the conifer snags in the north (95%) and south (80%) subregions were on hillslopes (percentages account for difference in hillslope and valley floor sample area).

Density of hardwood snags was mostly much less than that of conifer snags in the central and south subregions (Table 4). In the north subregion, the difference between hardwood and conifer snag densities depended on stream order and distance from stream. Overall density of hardwood snags within 32 m of the stream was about three or more times greater at sites in the north subregion than at those in the central or south subregions (Table 4). Hardwood snag densities in the south subregion were highest at sites along third-order streams. A majority of the hardwood snags in the north (55%) and south (70%) subregions were on valley floors (percentages weighted by sample area).

Canopy cover

The association between canopy cover and topographic position was similar in each subregion. Cover of deciduous

Table 2. Percentage of total basal area for species comprising at least 5% of basal area by subregion, stream order, and distance from stream.

		First order			Second order				Third order				Fourth and fifth orders			
Subregion	Species	4 m	16 m	32 m	4 m	16 m	32 m	48 m	4 m	16 m	32 m	48 m	4 m	16 m	32 m	48 m
North	**Conifers**															
	Douglas-fir	18	27	34	28	27	35	nc	19	36	50	58	data not collected			
	Sitka spruce	27	19	22	+	+	+	nc	—	—	—	—	data not collected			
	Western hemlock	12	18	22	+	+	—	nc	+	+	+	—	data not collected			
	Western redcedar	+	6	5	—	—	—	nc	+	+	—	+	data not collected			
	Hardwoods															
	Red alder	39	30	17	64	69	61	nc	59	49	40	29	data not collected			
	Bigleaf maple	—	—	—	+	—	+	nc	19	12	9	9	data not collected			
Central	**Conifers**															
	Douglas-fir	45	47	53	33	43	47	56	13	22	30	26	7	11	27	44
	Western redcedar	25	19	14	9	10	12	14	6	8	7	11	7	6	7	+
	Western hemlock	11	13	17	+	+	+	+	6	12	9	20	16	16	12	14
	Sitka spruce	+	+	+	+	+	+	+	10	15	21	20	26	24	17	29
	Hardwoods															
	Red alder	12	16	14	38	21	13	15	51	31	24	10	31	26	18	8
	Bigleaf maple	+	+	+	14	21	22	11	14	12	9	13	13	16	19	+
South	**Conifers**															
	Douglas-fir	22	34	44	22	24	36	nc	13	29	51	58	data not collected			
	Western hemlock	33	31	23	32	31	18	nc	+	+	6	7	data not collected			
	Port-Orford cedar	+	7	13	9	13	18	nc	+	+	+	7	data not collected			
	Western redcedar	21	13	5	+	+	+	nc	—	—	—	+	data not collected			
	Hardwoods															
	Red alder	8	+	5	7	+	—	nc	34	9	+	+	data not collected			
	Bigleaf maple	9	8	+	12	12	7	nc	29	28	14	9	data not collected			
	California laurel	+	+	+	17	17	19	nc	21	27	17	16	data not collected			

Note: nc, data not collected; +, species present but comprised less than 5% of basal area; —, species did not occur.

Table 3. Species composition (%) of basal area prism tallies in north and south subregions by topographic position.

	North[a]			South[b]		
Species	Floodplain	Terrace	Lower hillslope	Floodplain	Terrace	Lower hillslope
Conifers	27.0	19.5	58.3	9.5	38.6	70.2
Sitka spruce	18.9	3.5	8.8	—	—	—
Douglas-fir	2.7	12.5	38.8	—	22.9	42.5
Western hemlock	5.4	2.1	8.2	9.5	8.7	15.7
Western redcedar	—	1.4	2.5	—	2.8	2.6
Port-Orford cedar	—	—	—	—	3.8	8.6
Grand fir	—	—	—	—	0.4	0.6
Pacific yew[c]	—	—	—	—	—	0.2
Hardwoods	73.0	80.5	41.7	90.5	61.4	29.8
Red alder	54.1	68.0	39.1	80.9	22.9	2.4
Bigleaf maple	18.9	12.5	2.6	—	23.3	11.6
California laurel	—	—	—	4.8	14.2	14.8
Oregon ash[d]	—	—	—	4.8	1.0	—
Tanoak	—	—	—	—	—	1.0

Note: Dashes indicate that species did not occur.

[a] Total number of prism tallies (north): floodplain, 37; terrace, 144; lower hillslope, 801.

[b] Total number of prism tallies (south): floodplain, 21; terrace, 288; lower hillslope, 1932.

[c] *Taxus brevifolia* Nutt.

[d] *Fraxinus latifolia* Benth.

hardwoods and amount of open sky decreased from terraces to hillslopes, whereas cover of conifers increased (Fig. 5). Open sky ranged from 20 to 50% on valley floors. Tall-shrub cover was slightly greater on transition slopes than at other topographic positions. Cover of tall shrubs and deciduous hardwoods was highest in the north subregion for each topographic position, and generally declined from north to south (Fig. 5). Salmonberry (*Rubus spectabilis* Pursh), the dominant shrub species in most Coast Range riparian forests (Hibbs and Giordano 1996; Pabst and Spies 1998), reflected this trend as well. It averaged 33.5% cover in the north subregion, 24.6% in the central subregion, and 2.6% in the south subregion (data not shown). Conifer cover was highest in the south subregion for each topographic position except active floodplains (Fig. 5). Cover of evergreen hardwoods increased from floodplains to hillslopes in the south subregion.

Tree regeneration

Conifer tree regeneration occurred on about 9% of the plots in the north subregion and about 10% of the plots in the central subregion, compared with about 24% of the plots in the south subregion. It was concentrated almost exclusively at sites along first-order streams in the north subregion (Fig. 6). In the central subregion, it was distributed across all stream orders and was most frequent on lower hillslopes of sites along fourth- and fifth-order streams. In the south subregion, conifer regeneration was least common at sites along third-order streams and was less frequent on transition slopes than on valley floors or hillslopes for all stream orders.

CART analysis identified basal area of shade-tolerant conifers as the most important variable for distinguishing plots with and without conifer regeneration (Fig. 7). Subsequent splits in the classification tree show that regeneration was more likely with nominal cover of exposed logs, and where hardwood tree basal area was low, the gap in the conifer canopy over the stream was small, and shrub cover was less than 26%. The tree model was pruned to six terminal nodes using a cross-validation routine (Breiman et al. 1984) and accounted for 15% of the variation in the response variable. "Presence" of regeneration was predicted at one terminal node (Fig. 7). Predictor variables representing coarser spatial scales, such as subregion and stream order, did not factor into the pruned tree.

Where conifer regeneration was present, basal area of shade-tolerant conifers was at least twice that where it was absent (Table 5). In contrast, Douglas-fir basal area was similar at plots with and without regeneration in the central and south subregions. Cover of tall shrubs was similar on plots with and without regeneration in the north subregion, but salmonberry cover was less where regeneration was present (Table 5). Generally, conifer regeneration in the north and central subregions was more common where salmonberry cover was less than 20% (Fig. 8).

The occurrence of hardwood tree regeneration varied by subregion and topographic position. About 13% of the plots in the north subregion had hardwood regeneration. Nearly all occurrences were at sites along third-order streams, where it was most common on valley floors (Fig. 6). In the central subregion, about 5% of the plots had hardwood regeneration. It was more prevalent on valley floors than on hillslopes of sites along first- through third-order streams. Hardwood tree regeneration was most common in the south subregion, occurring on 29% of the plots and across the range of stream orders and topographic positions, except for transition slopes at sites along first-order streams (Fig. 6).

Species composition of tree regeneration also changed with subregion and topographic position. In the north subregion, bigleaf maple and red alder comprised the bulk of

Table 4. Mean density (stems/ha) of conifer and hardwood snags by subregion, stream order, and distance from stream.

		Distance		
Subregion	Stream order	0–16 m	16–32 m	32–48 m
Conifer snags				
North	First	5.6 (5.6)	25.1 (7.8)	nc
	Second	17.1 (6.1)	48.8 (14.0)	nc
	Third	0.0 (—)	9.8 (4.4)	29.3 (20.6)
	Overall	7.6 (2.9)	28.0 (6.0)	29.3 (20.6)
Central	First	14.5 (5.4)	24.3 (6.8)	iss
	Second	10.2 (3.0)	12.6 (2.9)	19.5 (5.5)
	Third	11.0 (3.0)	10.8 (3.3)	6.2 (3.4)
	Fourth and fifth	8.9 (3.6)	7.1 (3.3)	7.8 (4.2)
	Overall	10.7 (1.8)	13.9 (2.1)	17.1 (3.5)
South	First	6.5 (3.8)	40.7 (13.8)	iss
	Second	11.4 (6.0)	27.7 (5.5)	iss
	Third	4.9 (1.9)	22.8 (6.1)	30.4 (8.2)
	Overall	6.9 (2.0)	28.5 (4.8)	30.2 (7.4)
Hardwood snags				
North	First	8.4 (6.0)	22.3 (16.7)	nc
	Second	4.9 (3.3)	12.2 (6.9)	nc
	Third	19.5 (7.1)	14.7 (7.0)	4.9 (4.9)
	Overall	11.0 (3.4)	16.1 (6.0)	4.9 (4.9)
Central	First	0.9 (0.9)	2.1 (1.5)	iss
	Second	3.3 (1.2)	3.0 (1.6)	4.2 (3.1)
	Third	4.4 (1.8)	4.2 (1.8)	4.1 (2.8)
	Fourth and fifth	8.9 (2.3)	1.8 (1.8)	0.0 (—)
	Overall	3.7 (0.9)	2.9 (0.8)	2.8 (1.4)
South	First	1.6 (1.6)	3.3 (2.3)	iss
	Second	3.3 (2.3)	1.6 (1.6)	iss
	Third	4.9 (2.2)	5.7 (2.0)	4.3 (3.2)
	Overall	3.7 (1.3)	4.1 (1.2)	3.8 (2.8)

Note: Standard errors are given in parentheses. nc, data not collected; iss, insufficient sample size.

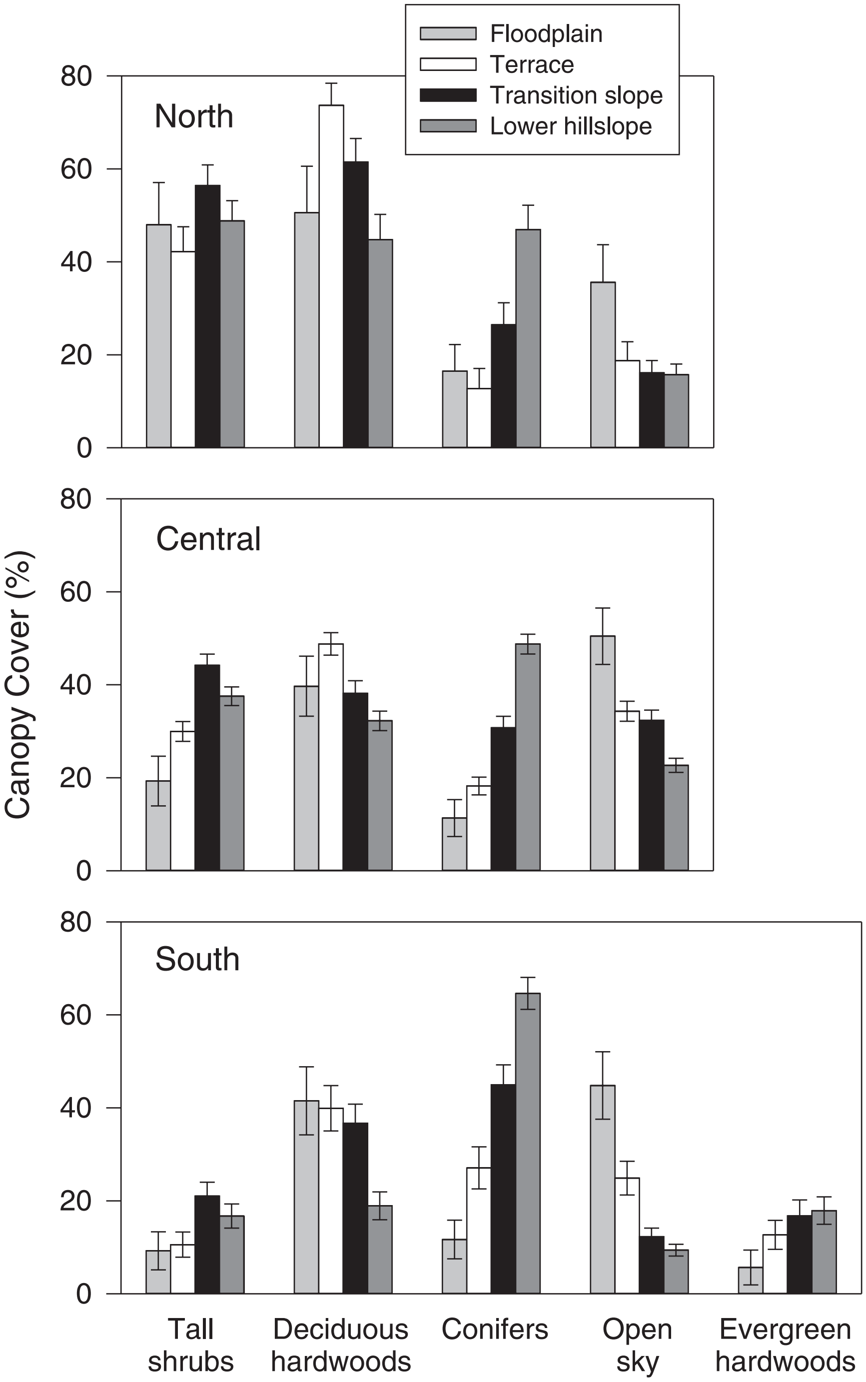
Table 5. Means by subregion of variables from plots where conifer tree regeneration was present and absent.

	North		Central		South	
Variable	Present (*n* = 13)	Absent (*n* = 131)	Present (*n* = 98)	Absent (*n* = 856)	Present (*n* = 73)	Absent (*n* = 227)
Basal area (m^2/ha)						
Shade-tolerant conifers	15.5 (4.8)	4.0 (0.7)	17.9 (1.7)	6.9 (0.5)	12.3 (1.6)	5.7 (0.7)
Douglas-fir	14.8 (4.4)	7.5 (0.9)	10.8 (1.7)	9.1 (0.5)	9.1 (1.3)	9.5 (0.9)
Hardwoods[a]	5.6 (2.4)	15.7 (1.0)	4.2 (0.6)	10.5 (0.4)	6.0 (0.9)	12.2 (0.8)
Canopy cover (%)						
Conifers	54.7 (10.6)	26.2 (2.8)	53.3 (4.1)	28.0 (1.3)	59.8 (4.5)	37.7 (2.6)
Hardwoods[a]	26.5 (11.6)	61.0 (2.9)	23.9 (3.7)	41.5 (1.4)	19.8 (3.8)	37.1 (2.6)
Tall shrubs	46.6 (9.6)	49.6 (2.7)	20.5 (3.1)	36.8 (1.3)	9.6 (2.2)	17.7 (1.8)
Salmonberry	17.8 (6.6)	35.0 (2.7)	12.4 (2.2)	26.0 (1.0)	0.9 (0.4)	3.1 (0.8)
Cover of exposed logs (%)	18.5 (6.6)	9.0 (1.0)	17.9 (2.1)	6.9 (0.4)	9.8 (1.4)	6.5 (0.6)

Note: Standard errors are given in parentheses.
[a] In the north and central subregions, all hardwoods were deciduous; in the south, there were deciduous and evergreen hardwoods.

regeneration occurrences on valley floors, whereas western hemlock and bigleaf maple were dominant on hillslopes (Table 6). Sitka spruce was more common on valley floors than on hillslopes, and Douglas-fir was found only on hillslopes. In the central subregion, valley-floor regeneration was dominated by red alder, with shade-tolerant conifer species comprising most of the rest (Table 6). Western hemlock was dominant on hillslopes. Douglas-fir regeneration was found infrequently in the central subregion. The south subregion had a greater diversity of regenerating tree species, including several {tanoak (*Lithocarpus densiflorus* (H. & A.) Rehd.), California laurel, California live oak (*Quercus*

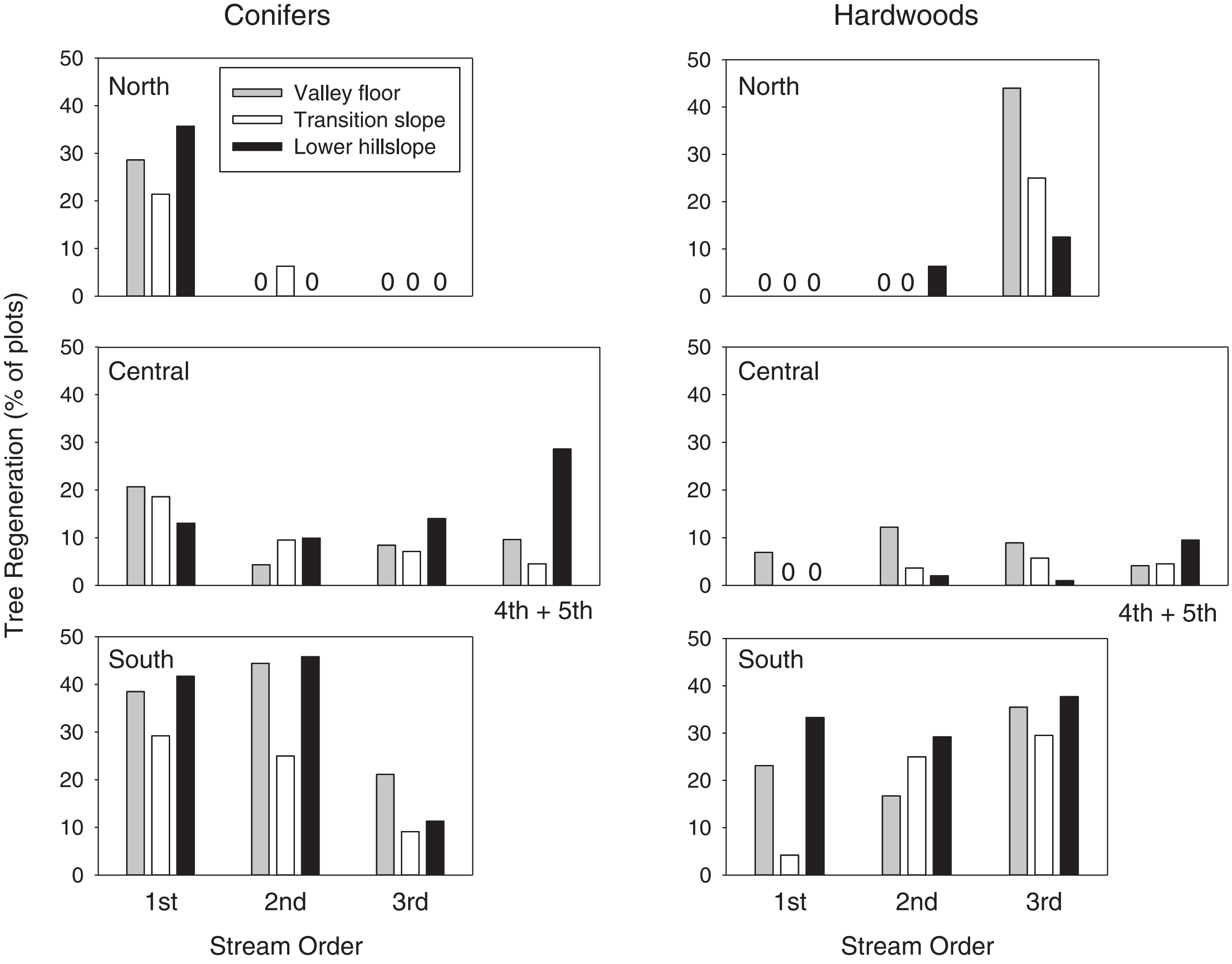
Fig. 5. Mean canopy cover by subregion and topographic position (canopy components were measured independently, so their sum could exceed 100%).



chrysolepis Liebm.), and Port-Orford cedar} that do not grow in the north or central subregions (Table 6). Red alder and Douglas-fir were the most common species on valley floors. On hillslopes, western hemlock was most common, followed by tanoak and California laurel; the latter two were noticeably less frequent on valley floors than on hillslopes.

The substrate for regenerating trees varied by subregion and species type. In both the north and central subregions, about 90% of the conifer regeneration was found on woody debris (downed logs or rotting snags), but in the south subregion, about 83% of the conifers were on mineral substrates (soil or gravel) or duff over soil (Fig. 9). Western hemlock comprised the majority of conifer regeneration in each subregion, and about 75% of the western hemlock regeneration in the south subregion was on mineral substrates or duff. Hardwood regeneration occurred almost exclusively (98%) on mineral substrates in the south subregion and mostly (68%) on mineral substrates in the central subregion, but in the north subregion, more hardwood regeneration was found on wood than on mineral substrates.

Fig. 6. Conifer and hardwood tree regeneration by subregion, stream order, and topographic position. Zeroes above *x* axes indicate absence of regeneration.



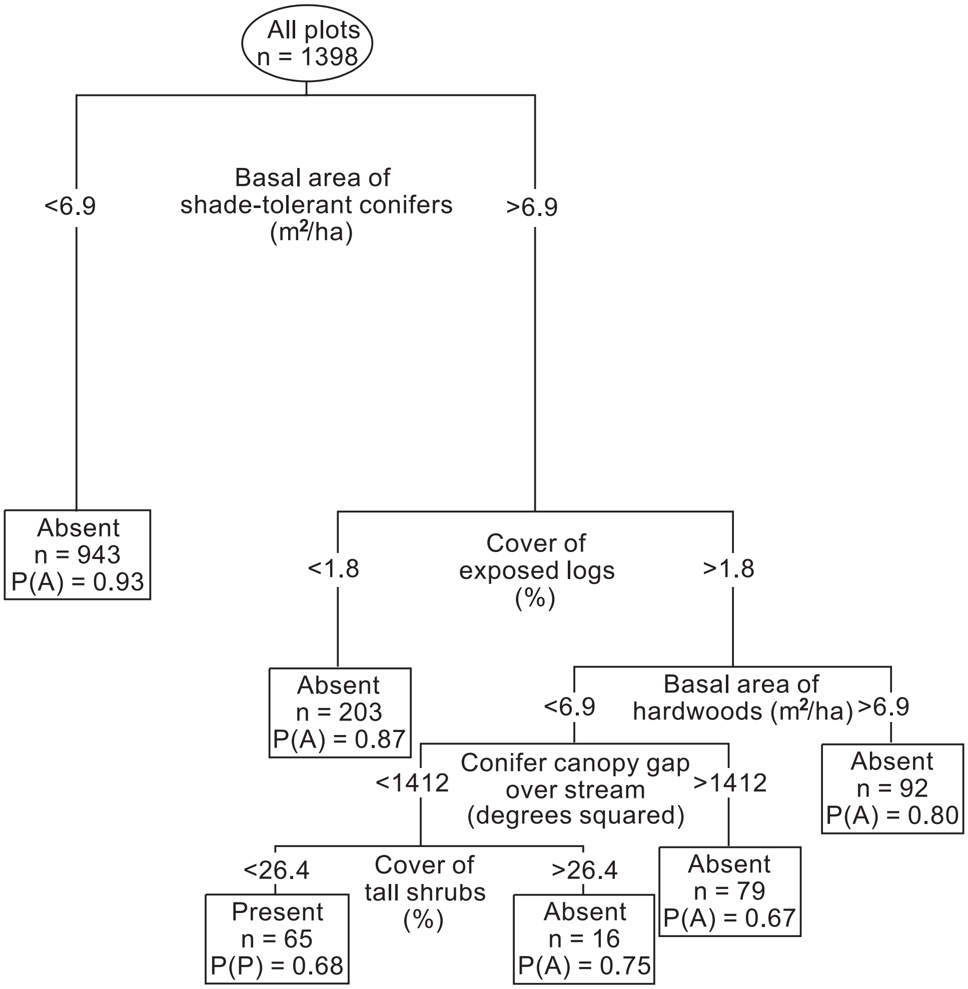
Discussion

Patterns in stand structure and composition

Stand structure and composition at the sites we sampled were heterogeneous at multiple scales; however, some clear trends emerged. The increase in conifer basal area with distance from stream implies a stream-to-hillslope environmental gradient that is probably associated with geomorphic, hydrologic, and topographic factors (Baker 1989; Bendix 1994). Average conifer basal areas at our sites ranged from about 10 m^2/ha at 4 m from the stream to around 30 m^2/ha at 48 m. These values are comparable with those reported by others (McGarigal and McComb 1992; Minore and Weatherly 1994) for unmanaged riparian forests in Oregon's coastal mountains and contrast with an average basal area of 54–66 m^2/ha for conifers in upland unmanaged forests in the Coast Range (Spies and Franklin 1991; McGarigal and McComb 1992). The difference can be attributed to lower densities of conifers near streams, as documented by others (Poage 1994; Nierenberg and Hibbs, in press) and as shown by our data on conifer snag densities. Hardwood basal areas showed little association with distance from stream, a pattern also documented in other studies (McGarigal and McComb 1992; Minore and Weatherly 1994).

The mechanisms responsible for patterns at the site scale likely change in relative influence with stream order (Hupp 1986; Naiman et al. 1992). Minore and Weatherly (1994) found that conifer basal area was positively correlated with elevation and stream gradient, and negatively correlated with stream width, all of which relate to stream order. In our study, conifer dominance of basal area along first-order streams probably reflects the geomorphic setting in this part of the drainage network. First-order streams in the coastal mountains are narrow and usually constrained by steep hillslopes that extend to near the stream edge. They have less influence on the surrounding environment than higher stream orders because floodplain development is limited or non-existent, and the canopy gap created by the channel is small (light levels may be only 1%–3% of full sunlight (Naiman and Sedell 1980)). However, conifer dominance does not necessarily indicate lack of disturbance or hydrological influence. Downcutting along these high-gradient streams can destabilize steep side slopes (Kelsey 1988), and downslope drainage can lead to permanently saturated soils

Fig. 7. Classification tree for presence–absence of conifer tree regeneration at the plot level in all subregions. Each split is labeled with its predictor variable and the splitting value. Terminal nodes (boxes) show the predicted response (absent or present), the number of plots (*n*) meeting the splitting criteria leading to the node, and the probability (*P*) that the predicted response will occur given the path leading to the node. The vertical distance between nodes is proportional to the amount of variation explained by the predictor variable associated with the split.



at the base of the slopes (Harr 1977). Such conditions may be unfavorable for conifers, as indicated by conifer basal area values that were lower at 4 m from the stream than at 16 and 32 m.

Hardwoods comprised a greater percentage of total basal area at sites along second- and third-order streams than at those along first-order streams. The valley bottoms of these larger, lower gradient streams were characterized by larger gaps in the conifer tree canopy, greater geomorphic and hydrologic (Reiter 1990) complexity, and less constraint on the stream course compared to first-order streams. This suggests that adaptations to both the fluvial environment and high or highly variable levels of soil moisture may be important in controlling tree species distributions. Indeed, conifers appear to lose the competitive advantage they hold in the uplands (Waring and Franklin 1979). Douglas-fir, for example, is relatively intolerant of high water tables (Minore 1979). Western redcedar and Sitka spruce can tolerate elevated soil moisture levels and inundation to various degrees (Minore 1970; Walters et al. 1980), but they were found only sporadically on valley floors. Their distribution may be limited by competition (Henderson 1978; Carlton 1988), herbivory (Minore 1990), seed source (Poage 1994), and the availability of favorable microsites for establishment (Harris 1990). In contrast, red alder, bigleaf maple, and a variety of shrubs have reproductive and physiological advantages that allow them to thrive in valley-bottom and lower slope settings (Pabst and Spies 1998).

Basal area data from sites in the central subregion indicate that near-stream (4-m) dominance of hardwoods may peak along third-order streams and then become secondary to conifers along fourth- and fifth-order streams. Several explanations are likely. Terraces along fourth- and fifth-order streams may be high enough above the water table (height above stream averaged 2.7 m in this study) and far enough removed from the influence of the stream to support conifers, including Douglas-fir. A contributing factor is that some large streams in the coastal mountains are effectively constrained by bedrock or downcutting (Schwartz 1990), which limits the stream's interaction with its floodplain or terrace. The prominence of Sitka spruce along larger streams may signify that effects associated with stream order and

Fig. 8. Relationship between conifer tree regeneration and salmonberry cover in the north and central subregions.

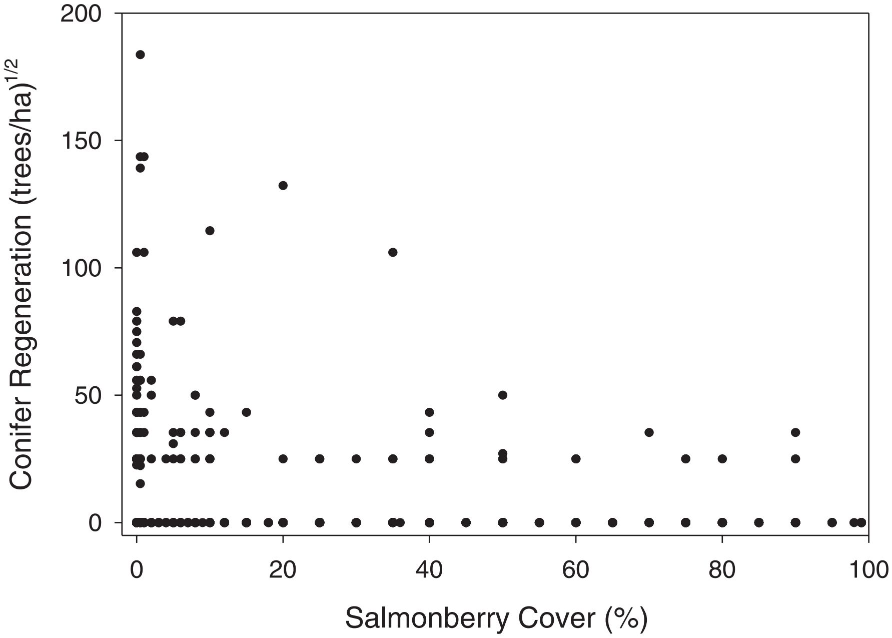


Table 6. Species composition (%) of tree regeneration by subregion and topographic position.

Species	North Valley floor	North Lower hillslope	Central Valley floor	Central Lower hillslope	South Valley floor	South Lower hillslope
Conifers						
Western hemlock	10.5	41.2	21.8	56.8	14.3	30.1
Sitka spruce	15.8	5.9	17.9	11.6	—	—
Western redcedar	—	—	10.3	10.5	1.3	2.7
Douglas-fir	—	11.8	2.6	4.2	23.4	6.2
Pacific yew	—	—	—	1.1	—	—
Port-Orford Cedar	—	—	—	—	5.2	4.4
Hardwoods						
Red alder	26.3	5.9	42.3	11.6	35.1	6.2
Bigleaf maple	42.1	29.4	5.1	4.2	13.0	5.3
Bitter cherry[a]	5.3	5.9	—	—	—	—
Tanoak	—	—	—	—	1.3	24.8
California laurel	—	—	—	—	2.6	17.7
Oregon ash	—	—	—	—	3.9	—
Canyon live oak	—	—	—	—	—	0.9
Cascara[b]	—	—	—	—	—	0.9
Pacific dogwood[c]	—	—	—	—	—	0.9

Note: Species composition was calculated as the percentage of the total number of plots in which regeneration of a species was present. Dashes indicate that species did not occur.

[a] *Prunus emarginata* (Dougl.) Walpers.

[b] *Rhamnus* spp.

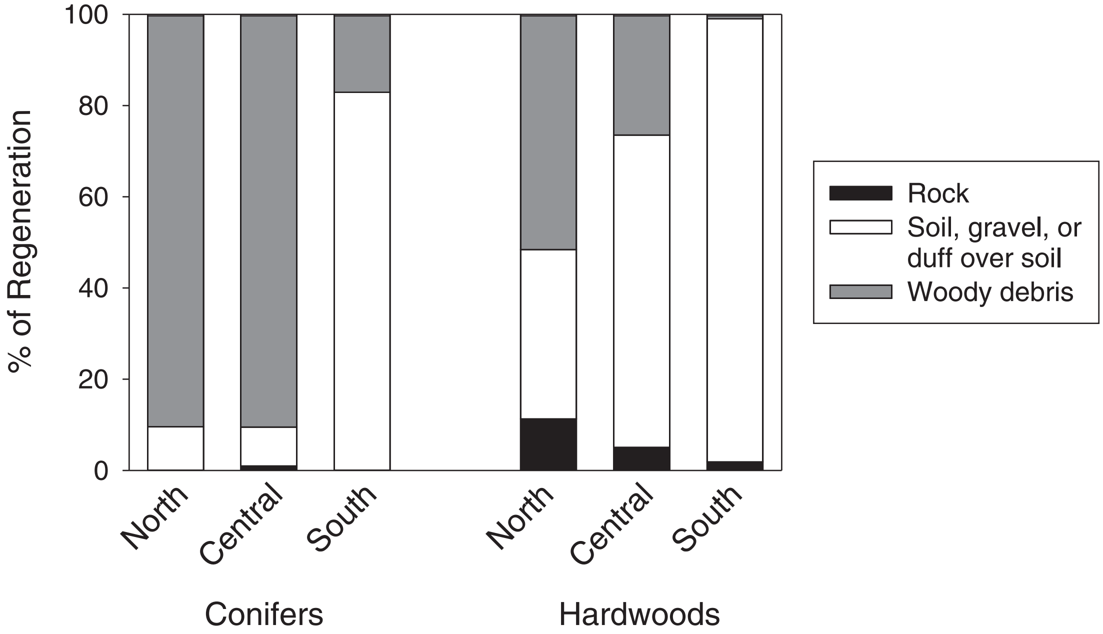
[c] *Cornus nuttalli* Aud. Ex T. & G.

soil moisture are confounded with the climatic influence of the ocean, which is not unusual since higher stream orders are generally closer to the coast and thus near or within the Sitka spruce vegetation zone.

Climate probably affects species distributions at the subregional scale (Ohmann and Spies 1998), even though forests in the study area generally are not temperature or moisture limited (Franklin and Dyrness 1973). Differences in species composition were evident in the south subregion as a whole, which is slightly warmer and drier in summer than the north and central subregions (Taylor 1993). Subregional differences in geology and soils distinguish the Klamath Mountains (south) from the geologically younger Coast Range (North and Central), so these factors could play a role in tree species distributions (Whitaker 1960). However, the effects may be masked or confounded by climatic differences (Ohmann and Spies 1998).

The north–south climatic gradient may influence the

Fig. 9. Substrate for conifer and hardwood tree regeneration by subregion.



distribution of red alder and salmonberry, two key riparian species of the coastal mountains (Hibbs and Giordano 1996; Pabst and Spies 1998). At sites in the north subregion, basal area data show that red alder was nearly as prominent on lower slopes as it was on valley floors, whereas in the south subregion it was abundant on floodplains, less abundant on terraces, and only a minor component on lower hillslopes. It appears that California laurel and bigleaf maple may replace the moisture-sensitive red alder (Harrington 1990) as the dominant hardwood species on lower slopes in the south subregion, although their distributions generally were patchier than that of red alder.

Salmonberry was much less abundant in the south subregion than in the north and central subregions. This may be a function of climatic differences; however, it could be confounded by salmonberry's response to canopy shading (Barber 1976; Pabst and Spies 1998), given the presence of evergreen hardwoods and higher cover of conifers in the south subregion. Unlike red alder, salmonberry apparently was not replaced by other species in the south subregion, since overall shrub cover was lower there than in the other subregions.

Tree regeneration

Our findings of low amounts of conifer tree regeneration are consistent with other recent studies (Minore and Weatherly 1994; Hibbs and Giordano 1996). Additionally, Minore and Weatherly (1994) found that the number of conifer seedlings was positively correlated with conifer basal area and negatively correlated with shrub cover and hardwood basal area. We found similar associations but also distinguished the basal area of shade-tolerant conifers from that of Douglas-fir. The latter was similar among plots with and without conifer regeneration in the central and south subregions, whereas the former was higher where regeneration was present in all subregions. This relationship is intuitive since most occurrences of regeneration were shade-tolerant species, but it underscores the importance of a local seed source (Schrader 1998).

Patterns in the occurrence of conifer regeneration across stream orders generally followed trends in conifer basal area. That is, it was more frequent at sites along low-order streams, where conifer basal area was highest. The exception, at sites along fourth- and fifth-order streams in the central subregion, was probably due to the proximity of those sites to the Sitka spruce zone.

Basal area of shade-tolerant conifers does not seem to explain differences in conifer regeneration at the subregional scale. In all subregions, shade-tolerant basal area was similar, and western hemlock was the most common regenerating conifer, yet regeneration was about 2.5 times more frequent in the south than in the other subregions. We hypothesize that competition from shrubs, particularly salmonberry, may be a key factor in limiting regeneration in the north and central subregions. Shrub cover also may account for the subregional differences in Douglas-fir regeneration, which was more frequent on valley floors in the south subregion (23% of occurrences) compared with the north (0%) and central (3%) subregions.

We were surprised to find that most of the western hemlock regeneration in the south subregion was on mineral substrates; this species typically is associated with wood substrates (Harmon and Franklin 1989), as we found in the north and central subregions. Where shrub cover is high, it is possible that the elevated seedbed of rotting logs and snags provides a less competitive environment than the forest floor. This is supported by Harmon and Franklin's (1989) findings that, in the absence of competition from herbs and thick moss, regeneration on soil could contribute substantially to tree recruitment in spruce–hemlock forests of coastal Oregon and Washington. Additional research is warranted to examine the distribution or availability of woody debris substrates at the landscape scale.

Our finding that hardwood regeneration occurred primarily on mineral substrates in the central and south subregions compared with wood substrates in the north subregion is due to differences in species composition. Red alder was the most common hardwood regenerating in the central and south subregions, whereas bigleaf maple, which germinates readily on wood (Minore and Zasada 1990), was most common in the north subregion.

It appears that broad-scale climatic, and possibly geologic, differences constrain the distributions of tree species at the scale of stream orders and sites. Similarly, factors that change with stream order, such as the extent of valley-floor landforms, are related to stand structure at the site level. However, we also found that some patterns seem more closely related to fine-scale processes associated with distance from stream (in the case of conifer basal area or snag density) and the local environment (in the case of conifer tree regeneration). These fine-scale patterns probably vary with regional setting and stream order. Thus, the overall patterns we observed may reflect an interaction among processes operating at multiple scales, such as that documented by Baker (1989) and Bendix (1994). In coastal riparian forests, this interaction is expressed as a patchy and variable mosaic of structure and composition.

Management implications

Data from this and other recent studies (Andrus and Froehlich 1988; McGarigal and McComb 1992; Minore and Weatherly 1994; Poage 1994; Nierenberg and Hibbs, in press) of unmanaged riparian forests in coastal Oregon provide baseline ecological information for managed riparian forests. These studies, representing a wide range of stand conditions, disturbance histories, geomorphic settings, and geographic locations, show that conifers typically do not dominate valley bottoms. Instead, shrubs and hardwoods such as red alder seem to have the competitive edge in most near-stream environments, and dominance of conifers appears to be limited to hillslopes. The abundance of red alder in present-day forests has been associated with logging disturbance (Harrington et al. 1994); however, the pollen record indicates that it has been abundant in the Coast Range for thousands of years (Worona and Whitlock 1995). It seems likely that riparian areas were the core habitat for this and associated species even in presettlement times.

The unmanaged riparian forests we studied do not necessarily provide appropriate references or targets for management. Our sites were not selected systematically or stratified randomly in proportion to subregion size, vegetation zone, or occurrence of stream orders. In addition, we focused on stands in mature or later stages of development and did not characterize earlier successional stages that might be encountered after major disturbance. We also cannot be sure that unmanaged forests in today's landscape represent the full suite of stand conditions from the recent past; for instance, there may have been preferential harvest of riparian areas with more conifers than areas we sampled. Thus, although we can provide a general picture of the variation in structure and composition within unmanaged riparian areas, we cannot say how representative that picture is across watersheds or subregions. Extrapolation of our findings to other sites and spatial scales must be done with caution. Ideally, management plans for streamside forests would be based more on how these forests function in aquatic and terrestrial environments and less on the notion of a reference condition. However, until those functions are better understood, our results can serve as a guide.

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