

INFLUENCES OF ENVIRONMENT AND DISTURBANCE ON FOREST PATTERNS IN COASTAL OREGON WATERSHEDS

MICHAEL C. WIMBERLY^{1,3} AND THOMAS A. SPIES²

¹Department of Forest Science, Oregon State University, Corvallis, Oregon 97331 USA

²U.S. Forest Service, Pacific Northwest Research Station, 3200 SW Jefferson Way, Corvallis, Oregon 97331 USA

Abstract. Modern ecology often emphasizes the distinction between traditional theories of stable, environmentally structured communities and a new paradigm of disturbance-driven, nonequilibrium dynamics. However, multiple hypotheses for observed vegetation patterns have seldom been explicitly tested. We used multivariate statistics and variation partitioning methods to assess the relative influences of environmental factors and disturbance history on riparian and hillslope forests. Our study area was the Cummins Creek Wilderness, located in the Oregon Coast Range. Most of the wilderness burned at least once between the mid-19th and early 20th centuries, creating a mosaic of younger forests with a few old-growth patches. Species composition on hillslopes varied primarily along a climatic gradient from moist maritime environments to drier inland climates but was relatively insensitive to forest age structure. The abundance of *Tsuga heterophylla*, a fire-sensitive, late-successional tree species, decreased with distance from old-growth patches, suggesting possible seed-source limitations following the historical fires. In contrast to species composition, hillslope forest structure was primarily related to fire history but was largely independent of environmental gradients. Old-growth structure characteristics such as large dominant trees, large snags, high down-wood volumes, and high tree size diversity increased with stand age and with the presence of remnant trees that survived the fires. Riparian forests had high shrub cover, abundant hardwoods, and high down-wood volumes, while the conifer-dominated hillslopes had high overstory density and basal area. Maritime climates and their associated plant species extended further inland in riparian areas than on hillslopes. Advance regeneration densities were higher in riparian forests within 5 km of the coast than in any other portion of the study area. Riparian forest structure and composition were related to both environmental and disturbance variables, with stream gradient and size integrating much of the fine-scale variability in disturbance regimes. No single theoretical framework was sufficient to explain the vegetation patterns observed in these forested watersheds. Our findings suggest a conceptual model of forest landscapes in which the relative influences of environment and disturbance on vegetation patterns are contingent on the facet of vegetation considered (composition vs. structure) and the portion of the landscape examined (hillslope vs. riparian).

Key words: community composition; Cummins Creek Wilderness, Oregon; environmental gradients; disturbance patterns; forest composition; forest structure; Oregon Coast Range; riparian forests; seed sources; succession.

INTRODUCTION

Community ecologists have long recognized the broad and sometimes bewildering array of ecological factors that influence forest succession and the resulting landscape patterns (Gleason 1926, Watt 1947, Pickett et al. 1987, Glenn-Lewin and van der Maarel 1992). Environmental conditions, available resources, and soil characteristics vary both in space and through time (Swanson et al. 1997). Disturbance regimes influence the spatial and temporal patterns of tree mortality and the creation of new sites for establishment (Pickett and White 1985). Community response to these factors de-

pends on the life-history characteristics of the component species, such as dispersal mechanisms, growth rates, and longevity (Noble and Slatyer 1980). A fundamental question in ecology asks how these multiple factors combine to drive succession and produce vegetation patterns at the landscape scale. Does the landscape's physical template exert the dominant influence on environmental variability, disturbance regimes, and the resulting vegetation? Or do disturbances generate a shifting mosaic in which the vegetation occurring at a particular site is largely unpredictable? To what extent do other factors, such as propagule availability, confound interpretations of vegetation relationships with the physical environment and prevailing disturbance regime?

Modern ecology often highlights a dichotomy between traditional theories emphasizing the role of environment in structuring orderly succession to stable

³ Present address: U.S. Forest Service, Pacific Northwest Research Station, 3200 SW Jefferson Way, Corvallis, Oregon 97331 USA. E-mail: mwimberly@fs.fed.us

vegetation communities (Clements 1936, Whittaker 1953), and a new paradigm in which disturbance is considered the dominant force structuring a complex and sometimes unpredictable forest mosaic (Pickett and White 1985, Wu and Loucks 1995). However, alternative hypotheses for observed landscape patterns have seldom been explicitly tested. Studies of forest community composition along elevation and topographic gradients have often downplayed the effects of disturbance by sampling only undisturbed old-growth vegetation (Whittaker 1956, Fonda and Bliss 1969, Zobel et al. 1976, del Moral and Watson 1978). Conversely, many studies of forest change following disturbance have either not considered environmental variability, or controlled for it by comparing sites within a limited range of environmental characteristics (Henderson 1978, Spies and Franklin 1991, Tyrrell and Crow 1994, Goebel and Hix 1997, Acker et al. 1998). In addition, most research has not encompassed the full range of ecosystem types found within forested watersheds. Studies have instead generally focused on either the patchwork patterns of upland forests (Heinselman 1973, Lertzman and Krebs 1991, Mladenoff et al. 1993, Frelich and Reich 1995), or on the longitudinal and latitudinal variation of riparian forests bordering the stream network (Baker 1989, Bendix 1994, Pabst and Spies 1999, Nierenberg and Hibbs 2000).

Only a few studies have explicitly compared the effects of multiple ecological factors on landscape-scale forest patterns. Their results suggest that the dominant factors controlling vegetation patterns vary with the extent of the study area and the manner in which vegetation is characterized. For example, Ohmann and Spies (1998) found that regional patterns of forest community composition in Oregon had strong relationships with climate, but had comparatively weak relationships with time since disturbance. In contrast, Weisberg (1998) found that forest structure was related to both disturbance history and physiographic setting in the Central Oregon Cascades. More comprehensive studies are needed to build a conceptual framework for understanding the complex pattern-process relationships inherent in forested landscapes.

Our research goal was to examine the relationships among forest patterns, environmental heterogeneity, and disturbance history in a coastal Oregon landscape, with particular emphasis on contrasts between riparian and hillslope vegetation. Because forest community patterns are influenced by multiple ecological processes, analyses based on mutually exclusive alternative hypotheses or simple null models can provide incomplete or misleading explanations for the patterns observed in complex landscapes (Quinn and Dunham 1983, Pickett et al. 1987). In contrast, the method of multiple working hypotheses (Chamberlain 1965) provides a framework for testing and ranking the influences of various causal factors. We used multivariate statistics combined with variation partitioning to de-

termine the dominant gradients of forest structure and composition and assess the relative importance of multiple ecological factors in structuring these vegetation patterns. We investigated the following set of nonexclusive working hypotheses.

Hypothesis 1: Vegetation patterns are structured by environmental gradients.—Studies of forest communities have traditionally considered environmental variability to be the predominant factor influencing vegetation. These relationships have often been conceptualized as an overlapping series of realized niches arrayed along one or more environmental gradients (Whittaker 1967). Forest vegetation research in mountainous regions has emphasized the importance of elevation, which influences temperature and precipitation, and topography, which affects soil moisture and exposure to solar radiation, as the primary physical gradients affecting community composition (Whittaker 1953, Fonda and Bliss 1969, del Moral and Watson 1978).

Hypothesis 2: Vegetation patterns are structured by disturbance.—Disturbances such as fires, floods, insect outbreaks, and windthrow kill patches of trees and create a mosaic of forest ages. The age-class distribution is an important component of forest pattern because both species composition (Connell and Slatyer 1977, Franklin and Hemstrom 1981) and forest structure (Heinselman 1973, Oliver 1981, Peet and Christenson 1987) change with time following disturbance. Also, because seeds of most tree species do not persist in the soil seed bank (Silvertown and Lovett Doust 1993), the mix of species that establishes after a disturbance may be linked to the abundance and spatial pattern of remnant seed sources that survive the disturbance (Reader et al. 1995, Clark et al. 1998).

Hypothesis 3: Vegetation patterns are structured through environmental control of disturbance.—Although individual disturbances are largely unpredictable, some aspects of disturbance regimes may be related to physical landscape features. For example, fires are infrequent in cool moist environments, but are often larger and more severe than the frequent, patchy fires that occur in warm, dry environments (Agee 1993, Morrison and Swanson 1990). Windthrow is most likely to occur on shallow soils or slopes exposed to prevailing winds (Ruth and Yoder 1953, Harris 1989, Nowacki and Kramer 1998). Patterns of flood disturbance vary throughout riparian networks depending on valley floor height and degree of channel constraint (Gregory et al. 1991, Grant and Swanson 1995). This spatial variability in disturbance regimes may then translate into spatial patterns of forest vegetation. For example, sheltered landforms with low fire frequencies may support high densities of fire-sensitive, late-successional species (Camp et al. 1997, Weisberg 1998), whereas flood-prone riparian landforms are likely to maintain plant communities dominated by early successional species (Sigafos 1961, Hupp 1982, Yanosky 1982).

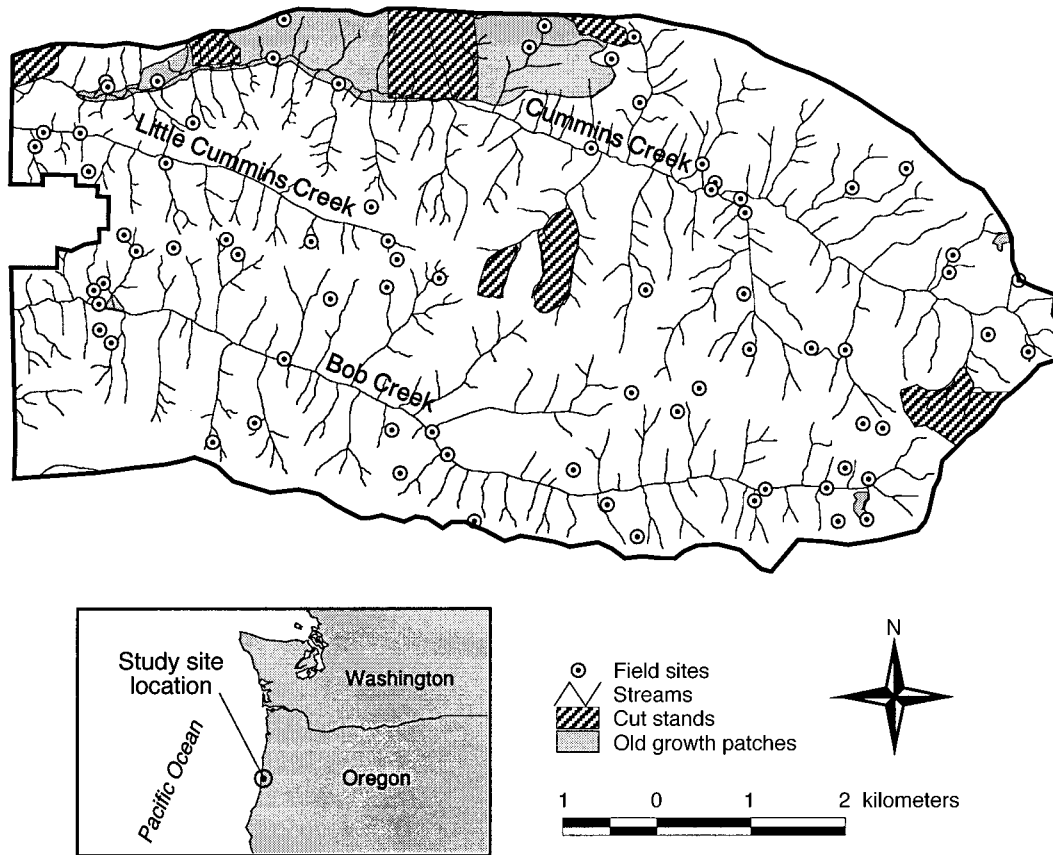


FIG. 1. Map of field site locations in the Cummins Creek Wilderness, Oregon. Cut stands were excluded from the analysis. Old-growth patches were delineated using aerial photographs.

METHODS

Study area

The 3900-ha Cummins Creek Wilderness (44°15' N 124°5' W) encompasses three forested watersheds on the central Oregon Coast (Fig. 1). The main stems of these watersheds flow from east to west, and empty directly into the Pacific Ocean. The area is mostly underlain by Yachats basalt, with deeply dissected terrain and steep slopes. Soils are mostly well-drained Andisols and Inceptisols. Elevation ranges from ~10 m near the coast to >800 m at the eastern boundary of the study area. Climate is characterized by abundant precipitation (180 cm/yr near the coast) with the majority falling during the winter months (November–March). Temperatures typically range from 10° to 20°C during the growing season, and rarely fall below freezing in the winter. Low-lying fog is common near the coast, and may extend several kilometers inland along river valleys (Franklin and Dyness 1988). Although precipitation increases with distance from the coast as air masses are lifted over the Coast Range, moisture stress is often lower near the coast because of cool summer temperatures and persistent fog.

In coastal areas, *Picea sitchensis* and *Tsuga heter-*

ophylla are the dominant tree species. Further inland, *Pseudotsuga menziesii* is the dominant overstory species, while *T. heterophylla* and *Thuja plicata* are less common but can be locally abundant. *Alnus rubra*, the major hardwood species, occurs in mixed stands with conifers, and is often the dominant tree species in riparian areas. *Acer macrophyllum* occurs less frequently, and is usually found on wide floodplains bordering the larger streams. Common understory species include *Rubus spectabilis*, *Vaccinium parvifolium*, *Gaultheria shallon*, and *Polystichum munitum*.

Cummins Creek, like most of the Coast Range, was affected by a series of large fires occurring between mid-19th and the early 20th centuries. These burns have created a landscape mosaic dominated by even-aged forests ranging from 70 to 120 yr in age. Remnant trees (defined as trees >200 yr in age that survived the wildfires) are rare, and are concentrated in a few old-growth patches (defined as patches with >3 remnant trees per hectare) scattered throughout the wilderness (Fig. 1). These old-growth patches have at least two distinct cohorts: One comprised of remnant trees, and another comprised of trees that established after the most recent fire. Less than 5% of the study area has

been cut, mostly around its perimeters—these harvested areas were excluded from the present study.

Vegetation data

We collected data from 72 field sites during the summer of 1997 using a stratified random sampling design (Fig. 1). We divided the landscape into two geographic zones (<5 km from the coast and >5 km from the coast) and five topographic zones (high-order riparian areas encompassing third- and fourth-order streams, low-order riparian areas encompassing first- and second-order streams, lower hillslopes, middle hillslopes, and upper hillslopes). Hillslopes were further subdivided into two aspect zones (north and south aspects). We created a map of these zones using a geographic information system (GIS), and randomly selected 4 sites in each of 12 hillslope strata (2 geographic zones \times 3 topographic zones \times 2 aspect zones) and 6 sites in each of 4 riparian strata (2 geographic zones \times 2 topographic zones). Only five of these randomly selected sites fell within old-growth patches (patches containing trees >200 yr old). To increase the number of old-growth sites in our sample, we sampled three additional sites located within old-growth patches during the summer of 1998. These sites were randomly selected using an old-growth map derived from aerial photographs (Fig. 1).

We located sites in the field using topographic and vegetation maps. After finding the approximate location of each hillslope site, we established the center at a random distance and offset to reduce observer bias in site selection. We established the center of each riparian site on the valley floor at a random location between the stream channel and the constraining footslope. Because valley floors were typically narrow in the first- and second-order streams (<10 m in width), the low-order riparian sites mostly encompassed the adjacent footslopes. Most of the high-order riparian sites were located entirely on the broad valley floors of third- and fourth-order streams (20–140 m in width), although some also overlapped the adjacent footslopes. The centers of all sample sites were georeferenced using a Trimble Pathfinder Pro XR Global Positioning System (GPS; Trimble Navigation Limited, Sunnyvale, California).

Each sample site encompassed \sim 0.25 ha, and was subsampled using three systematically located sets of nested circular plots. We sampled live trees (\geq 5 cm diameter at breast height [dbh]) and snags (\geq 10 cm dbh and \geq 2 m height) in 333-m² plots. We recorded dbh and species of live trees, and dbh of snags. Each live tree was also classified as either overstory (<50% of crown length beneath the level of the main canopy) or understory (\geq 50% of crown length beneath the level of the main canopy). We sampled seedlings (\geq 10 cm and <1 m height) and saplings (\geq 1 m height and <5 cm dbh) by species in 167-m² plots. We estimated percent shrub cover by species in 20-m² plots using eight

cover classes based on an arcsine square-root transformation of percent cover (Muir and McCune 1987). Within each set of nested plots, we measured down-wood volume along a 20-m transect using the line intercept method. We measured percent high shrub cover (\geq 1.5 m height) at three points along the transect using a moosehorn (Mueller-Dombois and Ellenberg 1974). Plot measurements were slope-corrected and aggregated to the site level.

Environmental data

On hillslopes, we measured slope along the steepest line of descent, whereas in riparian areas we measured slope as the channel gradient. We also measured valley floor width in riparian areas as the total distance between constraining footslopes, taken perpendicular to the stream. We computed additional environmental variables in a GIS. The GPS locations of sample sites were converted into a GIS point data layer, and the site locations were then overlaid on a U.S. Geological Survey 30-m digital elevation model (DEM). Elevation was obtained directly from the DEM. We computed a slope curvature index in Arc/Info Grid to distinguish convex landforms (high index values) from concave landforms (low index values). Slope position was computed using an algorithm that interpolated between valley bottoms and ridges: Values ranged from 0 (valley bottoms) to 100 (ridgetops). Total solar radiation input during the growing season (May–September) was calculated using the SolarImg program (M. Harmon, *unpublished software*). Topographic moisture index (Beven and Kirby 1979) was calculated as a function of drainage area and slope. We used the DEM to determine the approximate location of the coastline and computed distance from each site to the coastline in Arc/Info Grid. We used a detailed stream layer provided by the Siuslaw National Forest to classify streams by stream order. Distance to each site from the nearest stream was computed in Arc/Info Grid.

Disturbance data

Land survey records from the late 19th and early 20th centuries indicated that most of the Cummins Creek landscape was covered by shrub fields or stands of young trees. Exploratory analysis of several sites within the study area indicated that stands typically had unimodal age distributions. These results suggested that the forests were predominantly even-aged, having established after one of the historical wildfires between 1850 and 1920. Although some sites probably experienced subsequent fires following stand initiation, it is difficult to distinguish variability in age structure caused by repeat burns from other factors, such as seed source limitations or shrub competition (Franklin and Hemstrom 1981, Poage 1995). We therefore focused our tree-age sampling on determining the time since the last stand-replacing disturbance, and identifying any remnant trees that were present at each site.

We obtained increment cores at breast height from at least three overstory shade-intolerant trees at each site. *P. menziesii* and *P. sitchensis* were preferentially selected, although *T. heterophylla* and *T. plicata* were cored at a few locations where they were the only dominant conifers present. We first cored the largest shade-intolerant conifer at each site, and then cored several smaller conifers selected to span the range of overstory tree sizes. We also obtained several *A. rubra* cores at sites where this species was present. We mounted and sanded all the core samples and determined tree ages at breast height by counting annual rings under a dissecting microscope. When cores bypassed the pith we estimated tree age by extrapolating to the estimated pith based on the curvature of the annual rings. When trees were larger in radius than the length of our longest increment borer (42 cm), we estimated the number of years to the pith based on the width of the oldest annual rings on the core. Because trees were cored at breast height, ages represent the time since breast-height recruitment rather than seedling establishment. The time required to reach breast height probably varied depending on environmental conditions and the amount of competing vegetation at each site. Using breast-height cores from trees that established after clearcuts of known ages, we estimated that conifers generally required between five and fifteen years to reach breast height.

Stand age was assumed to be the age of the oldest tree at each site that had established after 1850, reflecting the approximate time since the last major fire. A few sites consisted of multiple cohorts, including a cohort of remnant trees (>200 yr old) that survived the wildfires, and a cohort of younger trees that established after the most recent fire. The presence of remnant trees at these sites was recorded as an indicator variable. We also recorded the presence of recent windthrow (trees snapped or uprooted in the direction of the prevailing winter storm winds), mass movement (evidence of recent landslides, slumps, or debris flows), and flood disturbance (significant scour or deposition from recent floods, or linear patches of streamside trees that established after previous floods) as indicator variables at each site.

We created a map of old-growth patches using 1995 color aerial photographs with a scale of 1:12 000 viewed through a mirror stereoscope. Areas were classified as old-growth patches if they were estimated to have three or more remnant trees per hectare. Old-growth patches were distinguished based on the presence of emergent tree crowns, dead tops, and multi-layered structure characteristic of old-growth canopies. Patch boundaries were delimited using acetate overlays on 1:25 000 scale orthophotos, and were verified in the field at several locations. The patch maps were digitized and converted to 30-m raster data layers, and the distance of each site from the nearest old-growth patch was computed using Arc/Info Grid.

Data analyses

We compared histograms of tree ages with accounts of historical fires obtained from independent sources, including General Land Office survey records from the late 19th century, homestead surveys made by the Siuslaw National Forest in the early 20th century, and published reports. We tested the null hypotheses that mean values of stand age, forest structure, and species abundance variables were similar in riparian areas and on hillslopes using two-sample *t* tests. Where necessary, we transformed the variables using either root or logarithmic functions. We examined advance regeneration patterns in greater depth by comparing the density and species composition of seedlings and saplings in coastal (<5 km from the coast) vs. inland (>5 km from the coast) forests. We tested the 2×2 contingency table for presence/absence of each disturbance class (old-growth remnants, mass movement, wind, disease, and flooding) vs. portion of the landscape (riparian vs. hillslope) using Fisher's exact test.

We used forward stepwise regression models to examine associations between disturbance variables and environmental variables, fitting separate models for the hillslope and riparian sites. We used multiple linear regression to model the continuous disturbance variables (stand age and distance from old growth). Independent variables were added to the regression models in order of decreasing error sum of squares reduction with $P < 0.05$ required for variables to enter based on a partial *F* test. We used multiple logistic regression to model the binary (presence/absence) disturbance variables. Independent variables were added to the regression models in order of decreasing reduction in deviance with $P < 0.05$ required for variables to enter based on a chi-squared test of the drop in deviance.

We used redundancy analysis (RDA) (terBraak and Prentice 1988) on a correlation matrix to carry out direct gradient analyses of woody plant community composition and forest structure as a function of environmental and disturbance variables. We computed separate ordinations for hillslopes and riparian areas. Root and logarithmic transformations were applied where necessary to enhance multivariate normality and decrease the influence of outliers. We used a forward stepwise method to select variables for each ordination with independent variables added in decreasing order of the total variance explained. We sequentially tested each independent variable's relationship with the vegetation variables against a null hypothesis of random association using a permutation test (terBraak and Smilauer 1998), with P values <0.05 required for variables to enter the model. We also used permutation tests to test the null hypothesis that the amount of variation explained by each ordination axis was no greater than expected under randomization (terBraak and Smilauer 1998).

We used the method of Okland and Eilertsen (1994)

to partition the variation explained by the ordinations into three categories, each corresponding to one of the three major working hypotheses outlined in the introduction:

E|D: Variation explained by environmental variables, independent of disturbance. (Hypothesis 1: Vegetation patterns are structured by environmental gradients.)

D|E: Variation explained by disturbance variables, independent of environment. (Hypothesis 2: Vegetation patterns are structured by disturbance.)

D∩E: Variation explained by disturbance variables and environmental correlates. (Hypothesis 3: Vegetation patterns are structured through environmental control of disturbance.)

Absolute estimates of variation explained by constrained ordinations are not strictly comparable among different data sets (Ohmann and Spies 1998, Okland 1999). We instead expressed the three categories as a percentage of the total variation explained (TVE).

RESULTS

Disturbance history

Historical records indicated that several major fires occurred in the vicinity of the Cummins Creek Wilderness. Between 1849 and 1952, one or more large fires burned ~325 000 hectares in the central Coast Range, including the Cummins Creek area (Morris 1934). In 1868, fires were reported near Yaquonia Bay, 35 km north of Cummins Creek. A previous fire history study found evidence of both these fires at sites <5 km from our study area (Impara 1997). In 1902, widespread fire blanketed the Pacific Northwest, with Coast Range fires reported at Newport, Tillamook, Mapleton, and Mary's Peak (Morris 1934). In addition, early 20th century survey maps of the western boundary of the Cummins Creek wilderness list some ridges as "burned in 1910."

Landscape age-structure analysis revealed a large gap in the age class distribution between trees that established before 1800 and trees that established after 1850 (Fig. 2). The reinitiation of overstory tree recruitment after 1850 indicated that most of the study area burned in the 1849 fire. In riparian areas and on lower hillslopes, breast height recruitment did not peak until after 1880 (Fig. 2a–c). Overstory recruitment was delayed even longer on middle and upper hillslopes, peaking between 1911 and 1920 (Fig. 2d, e). Recruitment in high-order riparian areas increased again between 1931 and 1940, and between 1961 and 1980 (Fig. 2a, b). These younger trees were all *A. rubra*, and were found on low floodplains close to the streams. The 1961–1980 recruitment pulse corresponded with major floods in 1964 (100-yr flood) and 1973 (50-yr flood).

Several lines of evidence suggest that multiple re-burns occurred in the study area, and may account for the delayed recruitment on the upper hillslopes. First, the peaks in overstory recruitment (after 1880 in ri-

parian areas and on lower hillslopes, and after 1910 in middle and upper hillslopes) followed historical Coast Range fires (1868 and 1902–1910). Comparison of General Land Office surveys conducted between 1879 and 1892 with current vegetation indicated that several areas burned and re-established in the early 20th century. In addition, survey notes from Forest Homestead Act applications between 1910 and 1920 explicitly mention multiple re-burns in the study area. One surveyor noted that: "These ridges have burned over numerous times, which has killed nearly all young timber growth, so that now practically all there is left is brush of different kinds and alder coming along in the canyon bottoms."

Differences between riparian and hillslope forests

Mean basal area and stand density were almost twice as high on hillslopes as in riparian areas (Table 1). Mean regeneration density was nearly five times as high in riparian areas as on hillslopes, but was also much more variable in the riparian areas. Down-wood volume, percent shrub cover, and percent hardwood basal area were also highest in riparian areas. Mean basal area of *A. macrophyllum* was higher in riparian areas than on hillslopes, while the mean basal area of *P. menziesii* was over eight times higher on hillslopes than in riparian areas. *Berberis nervosa*, *Gaultheria shallon*, and *Rubus ursinus* all had highest cover on hillslopes, while *Menziesia ferruginea*, *Ribes bracteosum*, and *Rubus spectabilis* had highest cover in riparian areas.

Mean stand age was higher in riparian areas than on hillslopes (Table 1). Sites with old-growth remnant trees were infrequent both in riparian areas and on hillslopes (Table 2). Evidence of flood disturbance was found in approximately half of the riparian areas. Mass movement occurred more frequently in riparian areas than on hillslopes, while windthrow was more common on hillslopes than in riparian areas. On hillslopes, stand age increased with slope and distance from the coast and decreased with elevation (Table 3). Hillslope sites on convex slopes tended to be located further from the nearest old-growth patch than sites on concave slopes. In riparian areas the probability of mass movement decreased with increasing stream order. The probability of flood disturbance increased as slope curvature became more concave, characterizing second- through fourth-order streams where the valley floor was tightly constrained by the surrounding hillslopes. Distance from the nearest old-growth patch was positively correlated with distance from the coast for the riparian sites. None of the other disturbance variables exhibited a statistically significant relationship with environmental variables.

Although overall advance regeneration density was highest in riparian areas, this pattern changed with distance from the coast. Within five km of the coast, seedling and sapling densities were almost an order of mag-

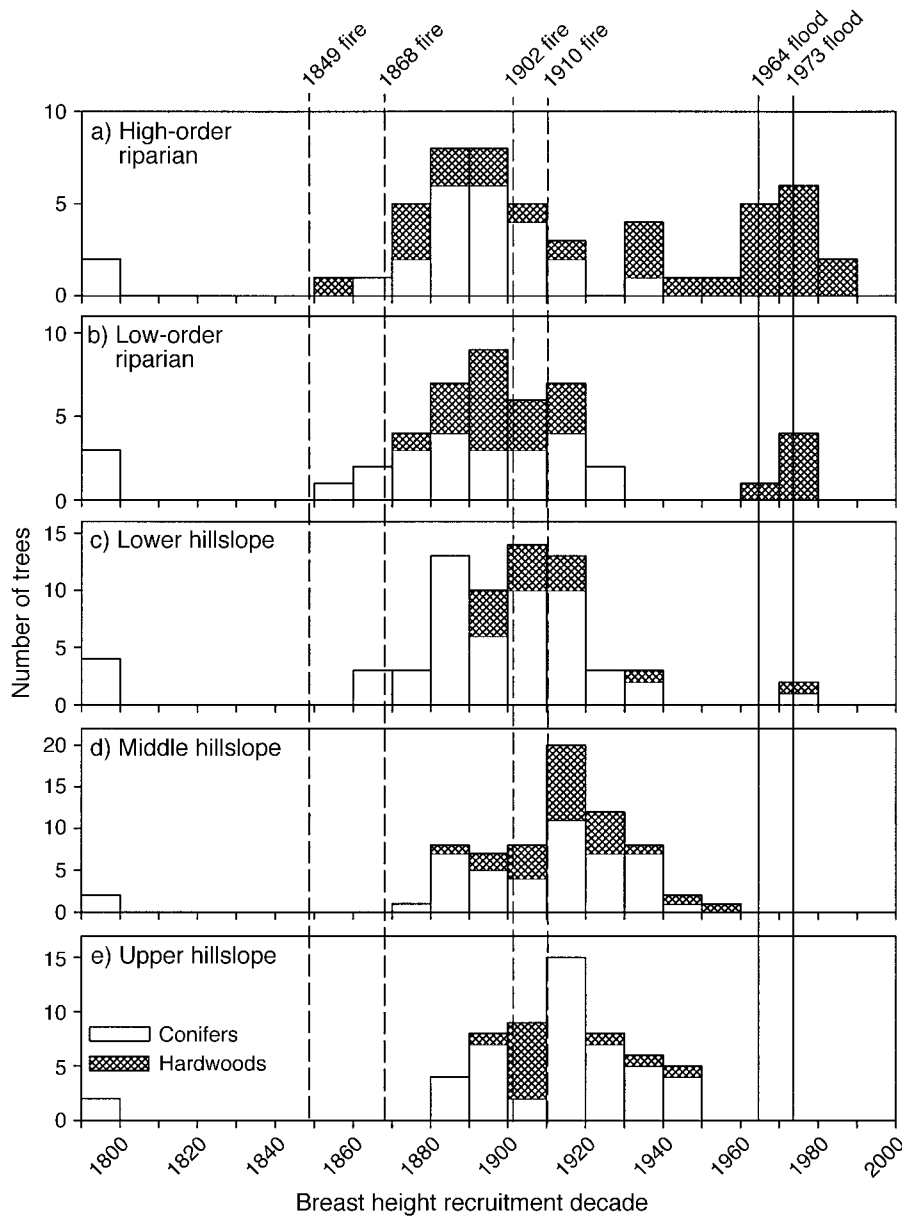


FIG. 2. Age class distribution of hardwoods and conifers by topographic position: (a) high-order riparian areas ($n = 50$), (b) low-order riparian areas ($n = 43$), (c) lower hillslopes ($n = 64$), (d) middle hillslopes ($n = 67$), and (e) upper hillslopes ($n = 55$). Individual bars represent the total number of trees sampled within each age class. The far left bars represent remnant trees established before 1800. Dashed lines denote historical fire years in 1849, 1868, 1902, and 1910. Solid lines represent recent flood years in 1964 (100-yr flood) and 1973 (50-yr flood).

nitude higher in riparian areas than on hillslopes (Fig. 3). At sites >5 km from the coast, however, riparian areas and hillslopes both had low densities of seedlings and saplings. *P. sitchensis* and *T. heterophylla* comprised the majority of seedlings and saplings (Fig. 4). Most advance regeneration within five km of the coast was *P. sitchensis*, although *T. heterophylla* percentages were also high. In contrast, most seedlings and saplings further than five km from the coast were *T. heterophylla*.

Species composition patterns

The stepwise RDA of hillslope community composition selected distance from the coast, elevation, distance from remnant patches, slope curvature, and growing season solar radiation as explanatory variables. The first hillslope axis reflected a gradient from high-elevation inland sites to low-elevation sites near the coast (Table 4). The high-elevation inland sites were dominated by *P. menziesii*, while the low-elevation coastal sites were characterized by *P. sitchensis* and *T. het-*

TABLE 1. Mean values (with standard errors in parentheses) of stand age, stand structure variables, tree species basal area, and shrub species cover for hillslope and riparian areas.

Variable	Hillslope ($n = 51$)	Riparian ($n = 24$)	P value
Stand age	101.7 (2.9)	115.9 (2.8)	0.003
Forest structure			
Basal area (m ²)	72.4 (4.3)	38.9 (5.6)	<0.001
Overstory tree density	281.4 (18.5)	158.8 (21.0)	<0.001
Large (>100 cm dbh) tree density	18.4 (3.0)	12.9 (2.8)	0.473
Understory tree density	52.0 (8.4)	37.9 (12.5)	0.319
Regeneration density	301.2 (104.9)	1445.0 (410.9)	0.005
Mean dbh (cm)	51.9 (1.8)	46.0 (2.9)	0.075
Std. dev. of dbh (cm)	27.5 (1.5)	31.3 (2.7)	0.193
Large (>50 cm dbh) snag density	8.7 (1.5)	6.9 (1.9)	0.605
Down wood volume (m ³)	704.0 (125.2)	1837.8 (236.0)	<0.001
Percent high shrub cover	13.3 (2.4)	27.9 (4.9)	0.003
Percent shade tolerant basal area	0.11 (0.02)	0.17 (0.04)	0.144
Percent hardwood basal area	0.13 (0.03)	0.34 (0.07)	<0.001
Tree species basal area (m ²)			
<i>Acer macrophyllum</i>	0.5 (0.3)	4.1 (2.1)	0.024
<i>Alnus rubra</i>	5.3 (1.1)	5.4 (1.0)	0.268
<i>Picea sitchensis</i>	8.6 (2.8)	15.6 (5.3)	0.108
<i>Pseudotsuga menziesii</i>	49.2 (4.8)	6.1 (2.0)	<0.001
<i>Thuja plicata</i>	1.6 (0.9)	1.0 (0.5)	0.874
<i>Tsuga heterophylla</i>	7.2 (1.7)	6.7 (2.5)	0.984
Shrub species cover (mean cover index)			
<i>Acer circinatum</i>	0.5 (0.2)	0.8 (0.3)	0.378
<i>Berberis nervosa</i>	1.1 (0.2)	0.3 (0.2)	0.009
<i>Gaultheria shallon</i>	1.7 (0.2)	0.8 (0.2)	0.014
<i>Menziesia ferruginea</i>	0.4 (0.1)	1.0 (0.2)	0.002
<i>Ribes bracteosum</i>	0.02 (0.02)	0.9 (0.2)	<0.001
<i>Rubus parviflorus</i>	0.4 (0.1)	0.2 (0.01)	0.235
<i>Rubus spectabilis</i>	1.8 (0.2)	3.2 (0.3)	<0.001
<i>Rubus ursinus</i>	0.5 (0.1)	0.08 (0.1)	0.015
<i>Sambucus racemosa</i>	0.6 (0.1)	1.0 (0.2)	0.072
<i>Vaccinium ovatum</i>	0.6 (0.2)	0.6 (0.2)	0.993
<i>Vaccinium parvifolium</i>	1.8 (0.1)	1.5 (0.2)	0.247

Notes: All variables are expressed on a per-hectare basis. P values are from two-sample t tests.

erophylla in the tree layer, and *Vaccinium ovatum* in the understory. We interpreted this axis primarily as a climatic gradient from relatively dry inland environments with high annual temperature variability to a moister maritime climate with lower annual temperature variability.

The first axis was also correlated with distance from remnant old-growth patches, with *T. heterophylla* and *P. sitchensis* basal area decreasing with distance from old-growth patches (Fig. 5). Multiple regression analysis indicated that *T. heterophylla* basal area had a

statistically significant relationship with distance from old growth even when relationships with other environmental and disturbance variables were taken into account (partial $R^2 = 0.16$, $P < 0.001$ with distance from the coast and presence of remnant trees already included in the model). The relationship between *P. sitchensis* and distance from old growth, however, was confounded by correlation with environmental and disturbance variables (partial $R^2 = 0.03$, $P = 0.15$ with distance from the coast, distance from streams, and presence of windthrow already included in the model).

The second hillslope axis reflected a gradient from high-elevation ridgetop sites with convex slopes to low-elevation, lower-hillslope sites with concave slopes (Table 4). We interpreted this axis as a topographic-moisture gradient. Moist sites were characterized by *T. plicata* in the tree layer and high cover of shrubs such as *Rubus parviflorus*, *R. spectabilis*, *Vaccinium parvifolium*, and *Acer circinatum*. In contrast, drier ridgetop sites were dominated by *P. menziesii* in the tree layer, and had low cover of all shrub species.

For riparian sites, stepwise RDA selected distance from the coast, elevation, and channel gradient as ex-

TABLE 2. Percentage of hillslope and riparian sites falling within each disturbance category.

Disturbance category	Hillslope (%) ($n = 51$)	Riparian (%) ($n = 24$)	P value
Remnant trees	9.8	12.5	0.701
Flooding	0	54.2	<0.001
Windthrow	23.5	4.2	0.050
Mass movement	5.9	33.3	0.004

Note: P values are from Fisher's exact test of the 2×2 contingency table of disturbance presence/absence vs. hillslope/riparian.

TABLE 3. Regression models of disturbance variables as a function of physiographic variables at riparian and hillslope sites.

Site	Regression equation	R ²
Hillslopes (n = 51)		
Stand age (yr)	stand age = 85.561 + 0.332(slope) + 0.00397(distance from coast) - 0.0634(elevation)	0.30
Distance from old growth (m)	square root(distance from old growth) = 27.059 + 8.016(slope curvature)	0.10
Riparian areas (n = 24)		
Distance from old growth (m)	square root(distance from old growth) = 13.681 + 0.00263(distance from coast)	0.17
Flooding	logit(flood) = -3.097 - 2.640(slope curvature)	0.52
Mass movement	logit(mass movement) = 3.107 - 1.666(stream order)	0.49

Notes: Linear regression models were used to predict stand age and distance from old growth. Logistic regression models were used to predict categorical disturbance variables. Variables were selected using a forward stepwise procedure with $P < 0.05$ required to enter. The R^2 for logistic regression equations was computed using the method of Nagelkerke (1991).

planatory variables. The first riparian axis was similar to the first hillslope axis, reflecting a climatic gradient from wet, low-elevation coastal sites dominated by *P. sitchensis* and *T. heterophylla* to drier, high-elevation inland sites dominated by *P. menziesii* (Table 4). However, climate was to some degree confounded by stream size because the largest, highest-order streams were found near the coast. This gradient was also correlated with distance from old-growth patches.

The change from *P. sitchensis* to *P. menziesii* dominated forests with distance from the coast occurred more rapidly on hillslopes than in riparian areas (Fig. 6). In riparian areas, *P. sitchensis* was the dominant conifer species from the coast up to four km inland. *P. menziesii*, in contrast, was not found in riparian areas <4 km from the coast, but dominated riparian forests >6 km inland. The proportion of *P. sitchensis* basal

area decreased more rapidly with distance from the coast on hillslopes than in riparian areas. *P. menziesii* was present on hillslopes at all distances from the coast, and became the dominant tree species at sites just two km inland.

The second riparian axis reflected a gradient from high-order streams to low-order streams (Table 4). The high-order streams had low gradients with frequent occurrence of flood disturbance, and were dominated by *A. macrophyllum* in the tree layer and *A. circinatum* in the shrub layer. Low-order streams had steep channels with frequent occurrence of mass movement disturbance. Plant communities along these streams were dominated by species usually associated with hillslope

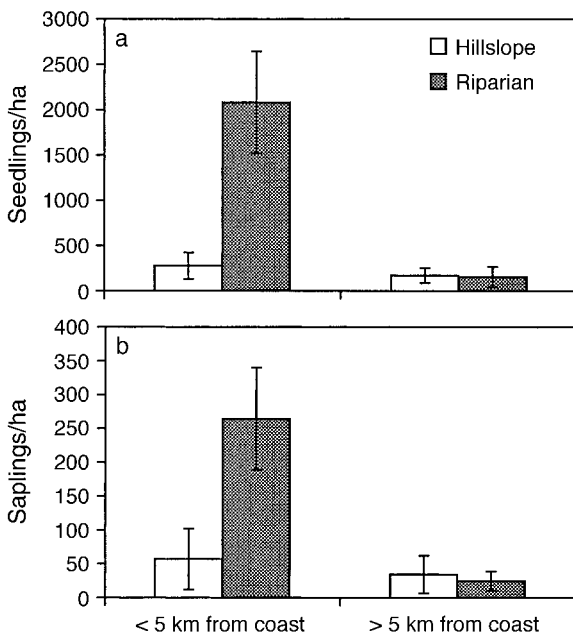


FIG. 3. Mean densities of (a) seedlings and (b) saplings (± 1 mean SE) for hillslope and riparian sites at inland and coastal locations.

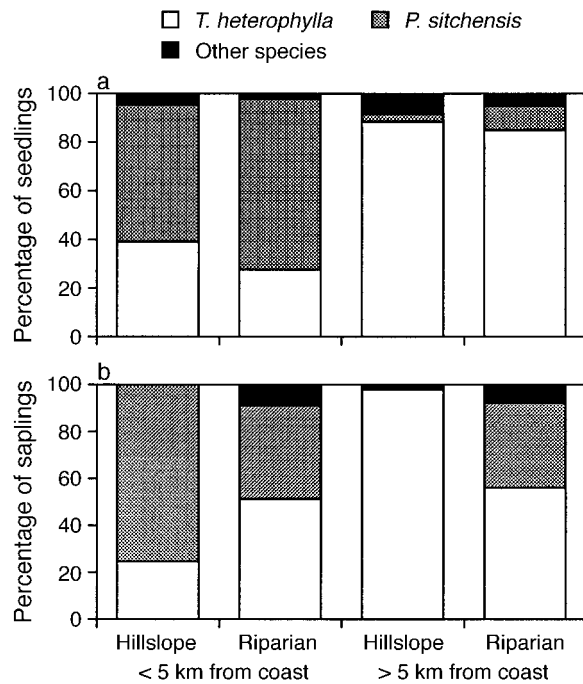


FIG. 4. Species composition of (a) seedlings and (b) saplings as a percentage of the total density of seedlings or saplings, summarized for hillslope and riparian sites at inland and coastal locations.

TABLE 4. Correlation of species, environment, and disturbance variables with the first two axes of the hillslope and riparian community composition RDAs.

Variable	Hillslope (<i>n</i> = 51)		Riparian (<i>n</i> = 24)	
	Axis 1	Axis 2	Axis 1	Axis 2
Percent variance explained	10.3	7.9	18.0	13.6
<i>P</i> -value	0.001	0.002	0.001	0.002
Species				
<i>Acer macrophyllum</i>	-0.11	0.26	0.05	-0.46
<i>Alnus rubra</i>	-0.01	0.26	0.30	0.05
<i>Picea sitchensis</i>	<u>0.70</u>	0.20	<u>-0.77</u>	0.17
<i>Pseudotsuga menziesii</i>	<u>-0.52</u>	-0.31	<u>0.71</u>	0.44
<i>Thuja plicata</i>	0.21	0.34	0.02	-0.01
<i>Tsuga heterophylla</i>	0.52	-0.19	-0.52	0.33
<i>Acer circinatum</i>	-0.25	0.31	-0.03	-0.31
<i>Berberis nervosa</i>	-0.14	-0.06	0.26	<u>0.76</u>
<i>Gaultheria shallon</i>	-0.26	-0.19	0.03	<u>0.65</u>
<i>Menziesia ferruginea</i>	0.16	0.14	-0.49	<u>0.23</u>
<i>Ribes bracteosum</i>	NA	NA	0.41	-0.23
<i>Rubus parviflorus</i>	-0.30	<u>0.55</u>	-0.22	0.14
<i>Rubus spectabilis</i>	-0.06	<u>0.43</u>	0.70	0.13
<i>Rubus ursinus</i>	-0.29	0.24	NA	NA
<i>Sambucus racemosa</i>	0.16	0.10	-0.02	-0.13
<i>Vaccinium ovatum</i>	0.42	0.07	-0.63	0.21
<i>Vaccinium parvifolium</i>	-0.09	<u>0.35</u>	0.08	<u>0.57</u>
Environment				
Elevation	-0.61	-0.62	0.88	0.44
Distance from coast	-0.74	-0.17	0.94	-0.34
Slope curvature	-0.21	-0.46	-0.24	0.55
Solar radiation	-0.29	0.06	0.08	0.54
Topographic moisture	0.42	0.11	0.02	-0.67
Slope angle	-0.04	0.37	0.58	0.74
Slope position	-0.19	-0.75	NA	NA
Distance from stream	-0.37	-0.44	NA	NA
Stream order	NA	NA	-0.28	-0.81
Valley floor width	NA	NA	-0.58	-0.27
Disturbance				
Stand age	-0.03	0.24	-0.29	0.18
Remnant trees	0.03	-0.19	-0.19	0.03
Distance from old growth	-0.50	0.39	-0.50	0.39
Mass movement	-0.04	0.32	0.02	0.59
Windthrow	0.33	-0.20	NA	NA
Flooding	NA	NA	0.12	-0.64

Notes: The *P* value for each axis is derived from a permutation test of the strength of association between the ordination axis and the vegetation variables. Underlined numbers represent the three strongest correlations between vegetation variables and the ordination axes. Boldface numbers represent the three strongest correlations between explanatory variables and the ordination axes.

environments, including *P. menziesii*, *G. shallon*, and *B. nervosa*. The prevalence of these species may have reflected the fact that sample sites along the lower-order streams tended to encompass more of the surrounding footslopes than the valley floor itself.

Forest structure patterns

The stepwise RDA of the hillslope forest structure selected stand age, presence of remnant trees, distance from remnant patches, slope curvature, and presence of windthrow as explanatory variables. The first hillslope axis reflected a gradient from young stands and stands located far from old-growth patches to older stands, stands with old-growth trees, and stands located close to old-growth patches (Table 5). Basal area, large tree density and standard deviation of dbh had the

strongest relationships with this axis; all increased with stand age, presence of remnants, and proximity to old-growth patches. Percent shade-tolerant basal area, mean dbh, large snag density, and regeneration density also increased with stand age, presence of remnants, and proximity to old-growth patches, but had weaker correlations with the ordination axis. We interpreted this axis as a gradient of increasing late-successional structure development with forest age (Spies and Franklin 1991). The correlation with distance from old growth reflected higher levels of *T. heterophylla* in the forest understory at sites close to remnant old-growth patches.

The second hillslope axis represented a complex gradient of age structure and topography. Younger stands and sites on convex landforms were generally found at

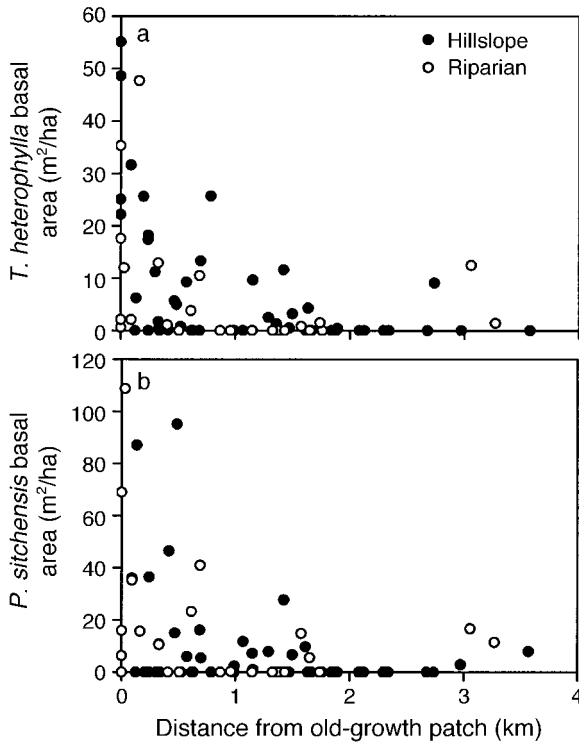


FIG. 5. Basal area per hectare of (a) *T. heterophylla* and (b) *P. sitchensis* as a function of distance from the nearest old-growth patch.

upper slope positions and had high-density conifer-dominated overstories with high basal area and few shrubs. Older stands and sites on concave landforms were found at lower slope positions and had low overstory densities with a high proportion of hardwoods, low basal area, and a dense shrub layer. We interpreted this axis primarily as a topographic-moisture gradient, with hardwoods and shrubs favored on concave landforms that collect soil moisture, and conifer stands with few shrubs favored on convex landforms that disperse soil moisture. The fourth hillslope axis (not shown) reflected a gradient from sites with windthrow and high volumes of down wood to sites without windthrow and low volumes of down wood.

In the riparian areas, stepwise RDA selected distance from the coast and stream order as explanatory variables. The first riparian axis reflected a gradient from coastal to inland sites (Table 5). The coastal sites were found at low elevations along streams with wide valley floors, and were generally closer to old-growth patches than the inland sites. Structural variation along this gradient was similar to that along the first hillslope gradient: Basal area, overstory density, large tree density, understory tree density, standard deviation of dbh, regeneration density, and percent shade-tolerant basal area were all highest near the coast and decreased with distance inland. Percent shrub cover and percent hard-

wood cover, in comparison, were lowest near the coast and increased with distance inland.

The second riparian axis reflected a gradient from high- to low-order streams (Table 5). High-order streams had wider valley floors, higher topographic moisture indices, and lower incidence of mass movement than low-order streams. Standard deviation of dbh and percent hardwood basal area increased with stream order, while percent shrub cover, understory trees per hectare, down-wood volume, and percent shade-tolerant basal area decreased with increasing stream order. This gradient reflected a variety of ecological factors that changed with stream size and channel gradient. High proportions of hardwoods along high-order streams probably reflected the abundance of *A. rubra* patches that established after floods, along with large *A. macrophyllum* that were mostly restricted to broad valley floors. The mixtures of smaller *A. rubra* with larger *A. macrophyllum* and conifers may have accounted for the greater variability in tree sizes along the high-order streams. Higher amounts of shade-tolerant conifers and understory trees (mostly conifers) along low-order streams may simply have reflected the

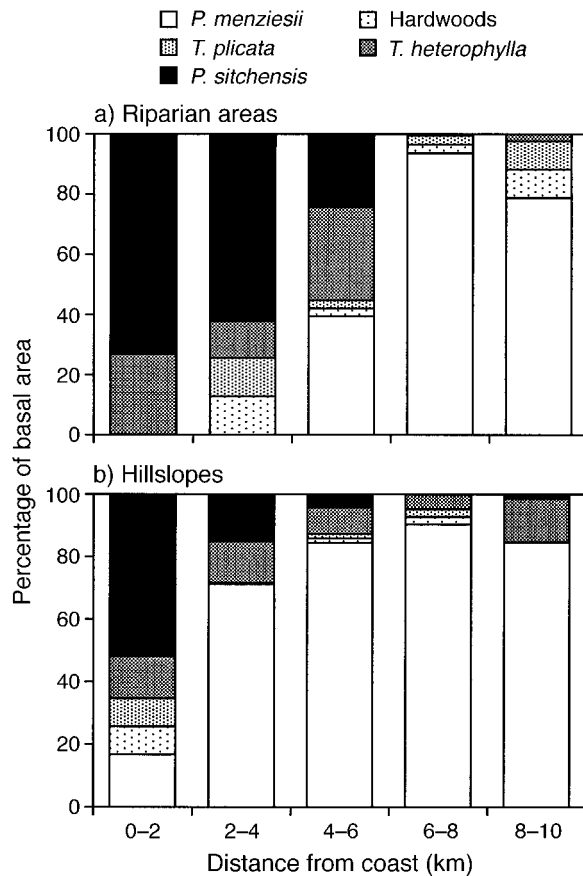


FIG. 6. Overstory species composition computed as a percentage of the total basal area within each landscape unit as a function of distance from the coast for (a) riparian areas and (b) hillslopes.

TABLE 5. Correlation of forest structure, environment, and disturbance variables with the first two axes of the hillslope and riparian forest structure RDAs.

Variable	Hillslope (<i>n</i> = 51)		Riparian (<i>n</i> = 24)	
	Axis 1	Axis 2	Axis 1	Axis 2
Percent variance explained	17.7	6.2	19.3	8.2
<i>P</i> value	0.001	0.032	0.003	0.025
Forest structure				
Tree density	<u>-0.84</u>	<u>-0.37</u>	-0.32	0.29
Mean dbh	<u>0.30</u>	<u>0.12</u>	-0.12	-0.11
Std. dev. of dbh	<u>0.76</u>	0.11	<u>-0.56</u>	-0.38
Basal area	<u>0.53</u>	-0.27	<u>-0.55</u>	0.02
Large tree density (>100 cm dbh)	<u>0.62</u>	0.21	<u>-0.49</u>	-0.04
Understory tree density	0.35	-0.07	-0.33	0.30
Regeneration density	0.31	0.02	<u>-0.66</u>	-0.06
Percent high shrub cover	-0.18	<u>0.46</u>	<u>0.65</u>	<u>0.44</u>
Large snag density (>50 cm dbh)	0.32	0.03	-0.21	0.15
Down wood volume	0.43	0.30	-0.07	0.31
Percent shade tolerant basal area	0.41	-0.15	-0.35	<u>0.40</u>
Percent hardwood basal area	-0.30	<u>0.35</u>	0.43	<u>-0.42</u>
Environment				
Elevation	-0.26	-0.13	0.79	0.35
Distance from coast	0.11	0.18	0.98	-0.21
Slope curvature	-0.18	-0.53	-0.46	0.43
Solar radiation	0.33	-0.16	-0.20	0.21
Topographic moisture	0.08	0.18	0.20	-0.73
Slope angle	0.11	0.39	0.30	0.74
Slope position	-0.11	-0.52	NA	NA
Distance from stream	0.03	-0.43	NA	NA
Stream order	NA	NA	-0.23	-0.97
Valley floor width	NA	NA	-0.66	-0.46
Disturbance				
Stand age	0.64	0.64	-0.46	0.18
Remnant patch	0.81	-0.18	-0.53	0.20
Distance from old growth	-0.68	0.40	0.67	-0.52
Mass movement	0.34	0.39	-0.10	0.69
Windthrow	0.15	-0.22	NA	NA
Flooding	NA	NA	0.19	-0.29

Notes: The *P* value for each axis is derived from a permutation test of the strength of association between the ordination axis and the vegetation variables. Underlined numbers represent the three strongest correlations between vegetation variables and the ordination axes. Boldface numbers represent the three strongest correlations between explanatory variables and the ordination axes.

higher overall proportion of conifers in these environments.

Relative importance of disturbance and environment

On hillslopes, environmental variables independent of disturbance (E|D) accounted for 74% of the explained variation in species composition, while disturbance variables independent of environment (D|E) accounted for 26% (Fig. 7). Disturbance variables and environmental correlates (D∩E) did not account for any of the explained variation in hillslope species composition. In contrast, D|E accounted for 85% of the explained variation in hillslope forest structure, while E|D accounted for 12% of the explained variation in hillslope forest structure, and D∩E accounted for the remainder. In the riparian areas, E|D accounted for 68% of the explained variability in species composition, while D|E accounted for 21% and D∩E accounted for 11%. When riparian forest structure was considered,

E|D accounted for 48%, D|E accounted for 29%, and D∩E accounted for 22% of the explained variability.

DISCUSSION

Recent disturbance history

The recent fire history of the Cummins Creek Wilderness supports the general hypothesis that topographic features have a relatively weak influence on the patterns of high-severity crown fires (Turner and Romme 1994). Remnant trees that survived the large, catastrophic fire of 1849 were no more common in riparian areas or moist sites than in other parts of the landscape. Topography, however, had a greater influence on the reburns that occurred after the large 1849 fire. Stands were generally younger on hillslopes than in riparian areas and younger on upper than lower hillslopes, indicating that dry sites had a higher probability of reburning than moist sites.

Several other researchers have documented high fire

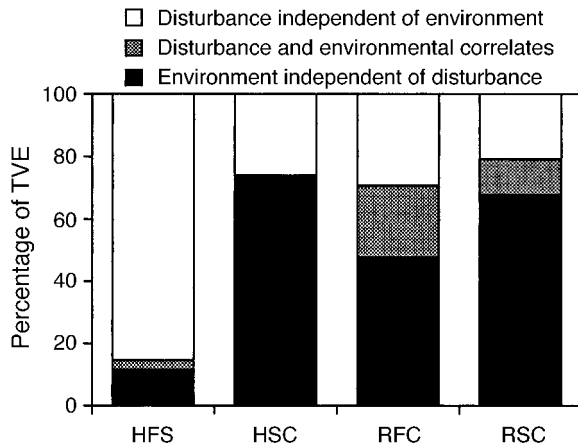


FIG. 7. Percentage of the total variation explained (TVE) accounted for by disturbance and environmental variables in the redundancy analysis ordinations. Variation partitioning was carried out using the method of Okland and Eilertsen (1994) for hillslope forest structure (HFS), hillslope species composition (HSC), riparian forest structure (RFS), and riparian species composition (RSC).

frequencies during the mid- to late 19th century, concurrent with European settlement, and these increases have been attributed to the warm, dry climate that prevailed at the end of the Little Ice Age (Weisberg 1998). Increased ignitions from land-clearing efforts may also have contributed to the high fire frequencies during this period. Although we found no direct historical references to human-caused fires in our study area, several lines of evidence suggest that burning by settlers may have contributed to the multiple fires in the Cummins Creek Wilderness. Our model of stand age on hillslopes predicted younger stands near the coast, contradicting the general assumption that moist, coastal forests rarely burn (Agee 1993). The young forests near the ocean may instead reflect higher ignition rates from fires set for clearing land. Several homesteads were established along the coast, just to the west of our study area, and settlers in this area used fire to clear land and maintain pasture for sheep and cattle (Hays 1976). If burning occurred during the summer months, it is possible that the prevailing westerly winds could have carried the fires inland and burned portions of the study area.

The occurrence of multiple reburns complicates our interpretation of relationships between stand age and vegetation characteristics. Most importantly, the range of stand ages cannot be interpreted as a true chronosequence. The oldest sites, with breast height ages >120 yr, probably established shortly after the 1849 fire, following a relatively long period without a major, stand-replacing disturbance. Younger sites experienced one or more additional burns after 1849. These multiple burns within a relatively short time probably affected soil characteristics, availability of seed sources, and density and composition of competing vegetation in

addition to simply delaying stand establishment (Agee 1993).

We found that percent shade-tolerant basal area, understory tree density (predominantly shade-tolerants), and advance regeneration density all increased with age in hillslope forests. Although these patterns suggest a gradual accumulation and growth of shade-tolerant regeneration over time (Schrader 1998), our fire history results point to an alternative explanation. If younger stands were subjected to multiple burns prior to establishment, then these burns may have reduced the densities of shade-tolerant, fire-sensitive species such as *T. heterophylla*. Low seed availability from mature shade-tolerants could then be another explanation for low regeneration density in the younger stands. It is not possible to disentangle the influences of time since disturbance and frequency of reburns in the present case, and we suspect that both of these factors are reflected in the stand-age variable.

Wind is widely recognized as a major disturbance in coastal forest ecosystems (Harris 1989, Nowacki and Kramer 1998). We found evidence of wind disturbance in ~25% of our hillslope sites. These sites were characterized by one or more trees that had been uprooted or snapped in a SW to NE direction, corresponding to winter storm winds. Windthrow severity was relatively low at all sites, leaving the majority of the canopy intact. We also observed several larger (>1 ha) patches of severe windthrow in the study area, but these patches occurred too infrequently to be effectively sampled by our random design. We suspect that the infrequent occurrence and low severity of windthrow partly reflect the present state of these forests: relatively young, even-aged stands with dense canopies of healthy trees (Harris 1989). The importance of windthrow in structuring landscape patterns will likely increase as these forests age and develop uneven canopies containing more trees with heart rot and other stem-weakening defects.

Riparian forests

Differences between riparian and hillslope forests were mostly similar to those reported previously (McGarigal and McComb 1992, Pabst and Spies 1999, Nierenberg and Hibbs 2000). Although riparian forests had low densities of large conifers and low overstory basal areas, they had higher volumes of down wood than the hillslopes. Flooding and mass movement disturbances in the riparian areas may have led to higher mortality of overstory conifers compared to the more stable hillslopes. Because these disturbances typically kill trees by undercutting or uprooting (Gregory et al. 1991), the dead boles enter the coarse woody debris pool as down logs rather than snags. Down wood accumulation in the riparian areas may also reflect the stream system's role in collecting and transporting woody debris (Benda 1990).

Previous research has emphasized the scarcity of co-

nifer regeneration in Coast Range riparian forests (Hibbs and Giordano 1996, Pabst and Spies 1999), and we initially expected that riparian areas would have less advance regeneration than hillslopes because of intense shrub competition and lack of shade-tolerant seed sources. Although the amount of regeneration we found in these riparian forests was indeed low at our inland sites (>5 km from the coast), the amount of regeneration on inland hillslopes was not significantly higher. We suspect that low seed availability for shade-tolerant species limited establishment on hillslopes, as well as in riparian areas. Dense overstory canopies and low amounts of down wood, an important substrate for seedlings, may have also restricted regeneration opportunities in hillslope forests.

Advance regeneration density along coastal streams (<5 km from the coast) was actually higher than on coastal hillslopes, and was an order of magnitude higher than along inland streams. One possible reason for these high regeneration levels is the unique environment of the coastal riparian areas. Summer fog along the coast reduces evaporative demand and contributes precipitation in the form of fog drip (Franklin and Dyrness 1988). These conditions are highly conducive to the regeneration and survival of drought-sensitive species such as *P. sitchensis* and *T. heterophylla* (Minore 1979). Fog extends furthest inland along coastal river valleys (Franklin and Dyrness 1988), and may partly explain why regeneration densities were so much higher in the coastal riparian areas than on the adjacent hillslopes. Numerous *P. sitchensis* and *T. heterophylla* seed sources along with low shrub cover compared to inland riparian areas probably also contributed to the abundant regeneration along coastal streams.

Landscape patterns

Hillslope community composition was primarily related to environmental variables. The comparatively weak relationship between species composition and disturbance history reflects the long life-spans of Pacific Northwest conifers, and the relatively slow process of succession in these forests (Franklin and Hemstrom 1981). Most tree and shrub species are present throughout all phases of stand development, although subtle shifts in composition do occur over time (Schoonmaker and McKee 1988, Halpern and Spies 1995). This result supports our first hypothesis, suggesting a gradient-based view of forest communities in which the species found at a given site depends mainly on the local physical environment (Whittaker 1967). The concept of relatively stable, ordered community patterns forms the basis for the use of plant community composition to classify habitat types (Cook 1996). Our results suggest that it is possible to make meaningful inferences about the environmental characteristics of a given site based on forest community composition.

As in other studies of Pacific Northwest forest vegetation (Fonda and Bliss 1969, Zobel et al. 1976,

DelMoral and Watson 1978, Ohmann and Spies 1998), we found that climate was an important factor influencing community composition. If dominance of *P. sitchensis* in the overstory layer is accepted as an indicator of maritime climates (Franklin and Dyrness 1988), we can infer that the coastal influence extends between four and six km inland along the stream valley, but no further than two km inland on the hillslopes. Although topography was previously found to have only a weak relationship with regional vegetation patterns in Oregon (Zobel et al. 1976, Ohmann and Spies 1998), we found strong correlations between topography and vegetation composition. The relatively small extent of our study area may have enhanced our ability to detect relationships between topography and vegetation. When broader areas are examined, the particular species or structures associated with a given topographic position may be diluted by larger scale variations in climate and disturbance history. Thus, even though topographic variables explain little regional variability in community composition, they still may influence forest patterns within a given watershed.

The decrease in *T. heterophylla* basal area with distance from old-growth patches suggested that seed-source limitations following the historical fires also influenced forest community patterns at the watershed scale. The current locations of old-growth patches represent areas where the severity of the 19th century fires was lower than in other portions of the landscape, and we hypothesize that more *T. heterophylla* survived the historical fires in these locations than in other portions of the landscape. The density of *T. heterophylla* seed dispersed into forest openings drops rapidly within several hundred meters from the source (Pickford 1929, Issac 1930, Gashwiller 1969). Therefore, higher seed availability following fire may account for the higher basal areas of *T. heterophylla* currently found near old-growth patches. These results must be interpreted cautiously because they are derived from correlations obtained within a single study area. Additional factors, such as shading by the remnant tree patches and variation in soil characteristics or substrate availability, might have also influenced the spatial pattern of *T. heterophylla*.

In contrast to the species composition patterns, hillslope forest structure was primarily related to recent disturbance history. Relatively little of the variation in forest structure was correlated with the physical environment. These relationships support our second hypothesis of a landscape mosaic in which disturbance controls the pattern of forest structures across the landscape, but the type of structure found in a particular place at a given time is not predictable based on physical landscape characteristics (Borman and Likens 1979, Turner et al. 1993). Age-related trends in structural development were similar to those described in previous studies (Spies and Franklin 1991, Acker et al. 1998). Sites with a cohort of remnant trees had more

late-successional characteristics than sites without remnants, indicating that forests may develop old-growth structure more rapidly following partial, as opposed to stand-replacing, disturbance. As discussed previously, relationships with stand age must be interpreted cautiously because age reflects variation in the number of reburns before stand initiation, as well as the time since stand initiation.

Although the first axis of our riparian structure ordination described an old-growth structure gradient similar to the first axis of the hillslope ordination, the riparian ordination had a stronger relationship with distance from the coast than with forest-age structure. This structural gradient partly reflects changes in community composition with distance from the coast. Large *P. sitchensis* in coastal riparian areas account for much of the high overstory basal area and large tree density in these forests, and abundant *T. heterophylla* accounts for the high proportion of shade-tolerant basal area and understory trees. Inland riparian areas, in comparison, tend to be mosaics of *A. rubra* patches, shrub patches, and a few large *A. macrophyllum* or *P. menziesii*. High shrub cover beneath the open canopy competes with conifer seedlings, limiting seedling establishment and the development of a shade-tolerant multilayered canopy. Given these differences, it seems unlikely that the inland riparian areas will develop old-growth structure similar to the coastal riparian forests over time.

A large body of research has emphasized the importance of fluvial disturbance in structuring riparian vegetation patterns (Hupp 1982, Gregory et al. 1991, Grant and Swanson 1995). We found that disturbance variables accounted for more than half of the TVE for riparian forest structure, but only 32% of the TVE for riparian forest composition. Our use of stand age, along with indicators for other disturbance types, probably limited our ability to characterize the complex riparian disturbance regimes. Thus, our findings may understate the roles that floods and debris flows play in forest dynamics along coastal streams. The relatively high proportion of TVE explained by environmental variables correlated with disturbance variables supports our third hypothesis of linkages between the physical environment and fluvial disturbances. We suspect that environmental variables may also capture some of the heterogeneity of responses to riparian disturbances that were not directly measured by our disturbance variables. For example, an individual flood event might remove the majority of streamside vegetation in a narrow, constrained reach, but disturb less vegetation in a broader, unconstrained reach (Hupp 1982, Grant and Swanson 1995). The degree to which floods influence vegetation also decreases with the height of valley floor landforms above the active channel (Sigafos 1991, Yanosky 1982). More detailed characterizations of riparian disturbance history will be required to comprehensively assess the relationships among geomorphology, riparian disturbance, and forest vegetation.

SYNTHESIS AND CONCLUSIONS

No single theoretical framework provided an adequate explanation for forest patterns in the Cummins Creek Wilderness. Environmental gradients (Hypothesis 1), disturbances (Hypothesis 2), and environmental controls over disturbance (Hypothesis 3) all played a role in structuring vegetation at the landscape scale. Our findings suggest a conceptual model in which the relative influences of environment and disturbance on forest vegetation are contingent on the facet of vegetation considered (composition vs. structure) and the portion of the landscape examined (hillslope vs. riparian). Community composition may be primarily related to environmental gradients, rather than disturbance, in ecosystems where most species rapidly colonize disturbed sites and survive for centuries. Stand structure, in contrast, is somewhat predictable based on the timing and severity of past disturbances. However, these disturbance patterns may be largely independent of the physical environment in fire regimes dominated by infrequent, high-severity events. There are also exceptions to these generalizations. For example, the landscape pattern of fire severity may affect the distribution of particularly disturbance-sensitive species, such as *T. heterophylla*.

Most studies of forest ecology in the Pacific Northwest have focused on upslope forests, and many of our notions about riparian forests are based on assumptions derived from this research (Gregory 1997). Our findings suggest that many such assumptions are erroneous. Disturbance, environment, and vegetation are more tightly linked in riparian areas than on hillslopes because of topographic constraints on the effects of frequent floods and mass movements. Maritime climates and their associated plant species extend further inland in riparian areas than on hillslopes. High levels of tree regeneration in coastal riparian forests suggest that rates and pathways of succession in these areas may differ considerably from other portions of the landscape. Efforts to analyze and model forest landscapes must consider the influences of multiple ecological factors on vegetation pattern and dynamics, address the riparian network as a distinctive component of the broader landscape mosaic, and recognize that forest composition and structure may respond differently to disturbances and environmental controls.

ACKNOWLEDGMENTS

We thank Colleen Grenz, Rebecca Hess, Nick Maetske, Rob Pabst, Leslie Trabant, and Anne Wimberly for field assistance. David Hibbs, Julia Jones, Bruce McCune, Rob Pabst, and John Tappeiner provided valuable comments on earlier drafts of the manuscript. Partial funding for this research was provided by the National Science Foundation through a Graduate Traineeship in Landscape Studies at Oregon State University (NSF grant # GER-9452810) and by the Northwest Forest Plan Program of the U.S. Forest Service Pacific Northwest Research Station.

LITERATURE CITED

- Acker, S. A., T. E. Sabin, L. M. Ganio, and W. A. McKee. 1998. Development of old-growth structure and timber volume growth trends in maturing Douglas-fir stands. *Forest Ecology and Management* **104**:265–280.
- Agee, J. K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C., USA.
- Baker, W. L. 1989. Macro- and micro-scale influences on riparian vegetation in western Colorado. *Annals of the Association of American Geographers* **79**:65–78.
- Benda, L. 1990. The influence of debris flows on channels and valley floors in the Oregon Coast Range, USA. *Earth Surface Processes and Landforms* **15**:457–466.
- Bendix, J. 1994. Among-site variation in riparian vegetation of the southern California Transverse Ranges. *American Midland Naturalist* **132**:136–151.
- Beven, K. J., and M. J. Kirby. 1979. A physically based, variable contributing area model of basin hydrology. *Hydrological Sciences* **24**:43–69.
- Borman, F. H., and G. E. Likens. 1979. Pattern and Process in a Forested Ecosystem. Springer-Verlag, New York, New York, USA.
- Camp, A., C. Oliver, P. Hessburg, and R. Everett. 1997. Predicting late-successional fire refugia pre-dating European settlement in the Wenatchee Mountains. *Forest Ecology and Management* **95**:63–77.
- Chamberlain, T. C. 1965. The method of multiple working hypotheses. *Science* **148**:754–759.
- Clark, J. S., E. Macklin, and L. Wood. 1998. Stages and spatial scales of recruitment limitation in southern Appalachian forests. *Ecological Monographs* **68**:213–235.
- Clements, F. E. 1936. Nature and structure of the climax. *Journal of Ecology* **24**:252–284.
- Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *The American Naturalist* **111**:1119–1144.
- Cook, J. E. 1996. Implications of modern successional theory for habitat typing: a review. *Forest Science* **42**:67–75.
- del Moral, R., and A. F. Watson. 1978. Gradient structure of forest vegetation in the Central Washington Cascades. *Vegetatio* **38**:29–48.
- Fonda, R. W., and L. C. Bliss. 1969. Forest vegetation of the montane and subalpine zones, Olympic Mountains, Washington. *Ecological Monographs* **39**:271–301.
- Franklin, J. F., and C. T. Dyrness. 1988. Natural Vegetation of Oregon and Washington. Oregon State University Press, Corvallis, Oregon, USA.
- Franklin, J. F., and M. A. Hemstrom. 1981. Aspects of succession in the coniferous forests of the Pacific Northwest. Pages 212–229 in D. C. West, H. H. Shugart, and D. B. Botkin, editors. *Forest succession: concepts and application*. Springer-Verlag, New York, New York, USA.
- Frelich, L. E., and P. B. Reich. 1995. Spatial patterns and succession in a Minnesota southern-boreal forest. *Ecological Monographs* **65**:325–346.
- Gashwiller, J. S. 1969. Seedfall of three conifers in West Central Oregon. *Forest Science* **15**:290–295.
- Gleason, H. A. 1926. The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* **53**:7–26.
- Glenn-Lewin, D. C., and E. van der Maarel. 1992. Patterns and processes of vegetation dynamics. Pages 11–59 in D. C. Glenn-Lewin, R. K. Peet, and T. T. Veblen, editors. *Plant succession: theory and practice*. Chapman and Hall, London, UK.
- Goebel, P. C., and D. M. Hix. 1997. Changes in the composition and structure of mixed-oak, second-growth forest ecosystems during the understory reinitiation stage of stand development. *Ecoscience* **4**:327–339.
- Grant, G. E., and F. J. Swanson. 1995. Morphology and processes of valley floors in mountain streams, Western Cascades, Oregon. Pages 83–101 in J. E. Costa, A. J. Miller, K. W. Potter, and P. R. Wilcock, editors. *Natural and anthropogenic influences in fluvial geomorphology*. American Geophysical Union, Washington, D.C., USA.
- Gregory, S. V. 1997. Riparian management in the 21st century. Pages 69–85 in K. A. Kohm and J. F. Franklin, editors. *Creating a forestry for the 21st century*. Island Press, Washington, D.C., USA.
- Gregory, S. V., F. J. Swanson, and W. A. McKee. 1991. An ecosystem perspective of riparian zones. *Bioscience* **40**:540–551.
- Halpern, C. B., and T. A. Spies. 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. *Ecological Applications* **5**:913–934.
- Harris, A. S. 1989. Wind in the forest of southeast Alaska and guides for reducing damage. General Technical Report **PNW-GTR-244**. U.S. Forest Service Pacific Northwest Research Station, Portland, Oregon, USA.
- Hays, M. H. 1976. The land that kept its promise: a history of South Lincoln County. Lincoln County Historical Society, Newport, Oregon, USA.
- Heinselman, M. L. 1973. Fire in the virgin forests of the boundary waters canoe area, Minnesota. *Quaternary Research* **3**:329–382.
- Henderson, J. A. 1978. Plant succession on the *Alnus rubra/Rubus spectabilis* habitat type in Western Oregon. *Northwest Science* **52**:156–167.
- Hibbs, D. E., and P. A. Giordano. 1996. Vegetation characteristics of alder-dominated riparian buffer strips in the Oregon Coast Range. *Northwest Science* **70**:213–222.
- Hupp, C. R. 1982. Stream-grade variation and riparian-forest ecology along Passage Creek, Virginia. *Bulletin of the Torrey Botanical Club* **109**:488–499.
- Impara, P. C. 1997. Spatial and temporal patterns of fire in the forests of the Central Oregon Coast Range. Dissertation. Oregon State University, Corvallis, Oregon, USA.
- Issac, L. A. 1930. Seed flight in the Douglas-fir region. *Journal of Forestry* **28**:492–499.
- Lertzman, K. P., and C. J. Krebs. 1991. Patterns of gap-phase replacement in a subalpine, old-growth forest. *Ecology* **73**:657–669.
- McGarigal, K., and W. C. McComb. 1992. Streamside versus upslope breeding bird communities in the central Oregon Coast Range. *Journal of Wildlife Management* **56**:10–23.
- Minore, D. 1979. Comparative autecological characteristics of Northwestern tree species—A literature review. General Technical Report **PNW-GTR-87**. U.S. Forest Service Pacific Northwest Research Station, Portland, Oregon, USA.
- Mladenoff, D. J., M. A. White, J. Pastor, and T. R. Crow. 1993. Comparing spatial pattern in unaltered and disturbed forest landscapes. *Ecological Applications* **3**:294–306.
- Morris, W. G. 1934. Forest fires in Western Oregon and Western Washington. *Oregon Historical Quarterly* **35**:313–339.
- Morrison, P. H., and F. J. Swanson. 1990. Fire history and pattern in a Cascade Range landscape. General technical report **PNW-GTR-254**. U.S. Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.
- Mueller-Dombois, D. H., and H. Ellenberg. 1974. Aims and methods of vegetation ecology. John Wiley and Sons, New York, New York, USA.
- Muir, P., and B. McCune. 1987. Index construction for foliar symptoms of air pollution injury. *Plant Disease* **71**:558–565.
- Nagelkerke, N. J. D. 1991. A note on a general definition of the coefficient of determination. *Biometrika* **78**:691–692.
- Nierenberg, T. R., and D. E. Hibbs. 2000. A characterization of unmanaged riparian areas in the central Coast Range of

- western Oregon. *Forest Ecology and Management* **129**: 195–206.
- Noble, I. R., and R. O. Slatyer. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio* **43**:5–21.
- Nowacki, G. J., and M. G. Kramer. 1998. The effects of wind disturbance on temperate rain forest structure and dynamics of southeast Alaska. General Technical Report **PNW-GTR-421**. U.S. Forest Service Pacific Northwest Research Station, Portland, Oregon, USA.
- Ohmann, J. L., and T. A. Spies. 1998. Regional gradient analysis and spatial pattern of woody plant communities of Oregon forests. *Ecological Monographs* **68**:151–182.
- Okland, R. H. 1999. On the variation explained by ordination and constrained ordination axes. *Journal of Vegetation Science* **10**:131–136.
- Okland, R. H., and O. Eilertsen. 1994. Canonical correspondence analysis with variation partitioning: some comment and an application. *Journal of Vegetation Science* **5**:117–126.
- Oliver, C. D. 1981. Forest development in North America following major disturbances. *Forest Ecology and Management* **3**:153–168.
- Pabst, R. J., and T. A. Spies. 1999. Structure and composition of unmanaged riparian forests in the coastal mountains of Oregon. *Canadian Journal of Forest Research* **29**:1557–1573.
- Peet, R. K., and N. L. Christenson. 1987. Competition and tree death. *Bioscience* **37**:586–594.
- Pickett, S. T. A., S. L. Collins, and J. J. Armesto. 1987. Models mechanisms and pathways of succession. *Botanical Review* **53**:335–371.
- Pickett, S. T. A., and P. S. White. 1985. Patch dynamics: a synthesis. Pages 371–384 in S. T. A. Pickett and P. S. White, editors. *The ecology of natural disturbance and patch dynamics*. Academic Press, New York, New York, USA.
- Pickford, A. E. 1929. Studies of seed dissemination in British Columbia. *Forestry Chronicle* **5**:8–16.
- Poage, N. J. 1995. Comparison of stand development of a deciduous-dominated riparian forest and a coniferous-dominated riparian forest in the Oregon Coast Range. Thesis. Oregon State University, Corvallis, Oregon, USA.
- Quinn, J. F., and A. E. Dunham. 1983. On hypothesis testing in ecology and evolution. *The American Naturalist* **122**: 602–617.
- Reader, R. J., S. P. Bonser, T. E. Duralia, and B. D. Bricker. 1995. Interspecific variation in tree establishment in canopy gaps in relation to tree density. *Journal of Vegetation Science* **6**:609–614.
- Ruth, R. H., and R. A. Yoder. 1953. Reducing wind damage in the forests of the Oregon coast range. Research Paper **PNW-RP-7**. U.S. Forest Service Pacific Northwest Research Station, Portland, Oregon, USA.
- Schoonmaker, P., and A. McKee. 1988. Species composition and diversity during secondary succession of coniferous forests in the western Cascade Mountains of Oregon. *Forest Science* **34**:960–979.
- Schrader, B. A. 1998. Structural development of late successional forests in the central Oregon Coast Range: Abundance, dispersal, and growth of western hemlock (*Tsuga heterophylla*) regeneration. Dissertation. Oregon State University, Corvallis, Oregon, USA.
- Sigafoos, R. S. 1961. Vegetation in relation to flood frequency near Washington D.C. U.S.G.S. Professional Paper **424-C**. U.S. Geological Survey, Reston, Virginia, USA.
- Silvertown, J. W., and J. Lovett Doust. 1993. Introduction to plant population biology. Blackwell Science, London, UK.
- Spies, T. A., and J. F. Franklin. 1991. The structure of natural young, mature, and old-growth Douglas-fir forests in Oregon and Washington. Pages 91–109 in L. F. Ruggerio, K. B. Aubry, A. B. Carey, and M. H. Huff, editors. *Wildlife and vegetation of unmanaged Douglas-fir forests*. General Technical Report **PNW-GTR-285**. U.S. Forest Service Pacific Northwest Research Station, Portland, Oregon, USA.
- Swanson, F. J., J. A. Jones, and G. E. Grant. 1997. The physical environment as a basis for managing ecosystems. Pages 229–238 in K. A. Kohm and J. F. Franklin, editors. *Creating a forestry for the 21st century: the science of ecosystem management*. Island Press, Washington, D.C., USA.
- terBraak, C. J. F., and I. C. Prentice. 1988. A theory of gradient analysis. *Advances in Ecological Research* **18**:271–317.
- terBraak, C. J. F., and P. Smilauer. 1998. *CANOCO Reference Manual and User's Guide to Canoco for Windows: Software for Canonical Community Ordination (Version 4)*. Microcomputer Power, Ithaca, New York, USA.
- Turner, M. G., and W. H. Romme. 1994. Landscape dynamics in crown fire ecosystems. *Landscape Ecology* **9**:59–77.
- Turner, M. G., W. H. Romme, R. H. Gardner, R. V. O'Neill, and T. K. Kratz. 1993. A revised concept of landscape equilibrium: disturbance and stability on scaled landscapes. *Landscape Ecology* **8**:213–227.
- Tyrrell, L. E., and T. R. Crow. 1994. Structural characteristics of old-growth hemlock-hardwood forests in relation to stand age. *Ecology* **75**:370–386.
- Watt, A. S. 1947. Pattern and process in the plant community. *Journal of Ecology* **35**:1–22.
- Weisberg, P. J. 1998. Fire history, fire regimes, and development of forest structure in the Central Western Oregon Cascades. Dissertation. Oregon State University, Corvallis, Oregon, USA.
- Whittaker, R. H. 1953. A consideration of climax theory: the climax as a population and pattern. *Ecological Monographs* **23**:41–78.
- Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. *Ecological Monographs* **26**:1–80.
- Whittaker, R. H. 1967. Gradient analysis of vegetation. *Biological Review* **42**:207–264.
- Wu, J., and O. L. Loucks. 1995. From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. *Quarterly Review of Biology* **70**:439–466.
- Yanosky, T. M. 1982. Effects of flooding upon woody vegetation along parts of the Potomac River flood plain. U.S.G.S. Professional Paper 1206. U.S. Geological Survey, Reston, Virginia, USA.
- Zobel, D. B., A. McKee, and G. M. Hawk. 1976. Relationships of environment to composition, structure, and diversity of forest communities of the Central Western Oregon Cascades. *Ecological Monographs* **46**:135–156.