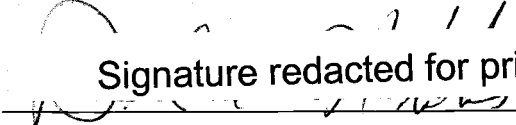


AN ABSTRACT OF THE DISSERTATION OF

Daniel A. Sarr for the degree of Doctor of Philosophy in Forest Science presented on November 22, 2004.

Title: Multiscale Controls on Woody Riparian Vegetation: Distribution, Diversity, and Tree Regeneration in Four Western Oregon Watersheds

Abstract approved:  Signature redacted for privacy.

David E. Hibbs

I studied riparian forests of four western Oregon watersheds (dry south to wet north) to determine the multiscale controls on woody riparian vegetation. I conducted separate analyses of controls on plant distribution, diversity, and tree regeneration using vegetation and environmental data collected in two related field studies: (1) a multiscale riparian forest inventory; (2) a comparative study of natural forest gaps and interiors.

Climatic moisture, indexed by vapor pressure deficit in summer, was the primary correlate of compositional change between riparian sites at all scales analyzed, demonstrating that the majority of riparian species responded directly or indirectly to the landscape scale climate gradient. Additional variation in composition was explained by measures of local topography and disturbance.

Climate, as indexed by modeled gross primary productivity (GPP), explained the majority of the variation in multiple regression models of plant diversity that included local and landscape scale variables. As GPP increased from dry to wet climates, understory light and moisture heterogeneity decreased,

coincident with declines in alpha, beta, and hectare scale diversity, suggesting that climate controls diversity indirectly through its effects on local conditions.

Tree regeneration varied sharply across the climate gradient; seedling frequency and diversity declined and nurse log use increased from the driest to wettest climates. Life history attributes of riparian tree species provided important clues to their regeneration success in different environments. These relationships were explored in a model that linked species shade and drought tolerance with expected variation in the environment caused by climate and disturbance. The model accurately predicted regeneration patterns for four of five functional groups of tree species.

The studies in this dissertation provided compelling evidence of regional variation in riparian vegetation composition, diversity, and dynamics, illustrating that these communities are strongly shaped by landscape scale as well as local scale factors. Moreover, climate-related differences among riparian sites were at least as important as the local variation within them in explaining spatial vegetation patterns. These findings argue for a multiscale perspective of riparian forest ecology that closely integrates larger scale controls, such as climate, with local hydrologic processes.

© Copyright by Daniel A. Sarr

November 22, 2004

All Rights Reserved

MULTISCALE CONTROLS ON WOODY RIPARIAN VEGETATION:
DISTRIBUTION, DIVERSITY, AND TREE REGENERATION
IN FOUR WESTERN OREGON WATERSHEDS

by

Daniel A. Sarr

A DISSERTATION

submitted to

Oregon State University

in partial fulfillment
of the requirements for the
degree of

Doctor of Philosophy

Presented November 22, 2004

Commencement June, 2005

ACKNOWLEDGEMENTS

I have received advice, support, and encouragement from many people over the six years since beginning this project. I extend my deepest gratitude to Dave Hibbs for inviting me to Oregon State, and for shepherding me faithfully down the long path this dissertation became. Throughout, Dave has been perceptive, patient, dedicated, and fun. The rest of my graduate committee also deserves recognition and thanks. Conversations with Dick Waring greatly increased my understanding of Pacific Northwest forest ecosystems. Mary Kentula, a fellow Swamp Thing, provided excellent advice about wetland and riparian areas and scientific writing whenever I was fortunate enough to visit her. Jim Wigington provided penetrating questions that challenged me to look broadly at riparian ecosystems and watersheds. Dominique Bachelet provided excellent comments that helped me write a more cogent dissertation.

I was fortunate to have the help of two outstanding field assistants, Rick Momsen and Peter Stocking. Thais Perkins and Ronasit Maneesai also provided skillful and much appreciated field help. Dennis Odion provided immensely helpful advice and much needed encouragement during the last stages of this dissertation. The Department of Forest Science was a fun and close-knit community where collaborations easily grew into friendships. Janet Ohmann, Rob Pabst, Jeff Shatford, and Jennifer Swenson were especially helpful, and the advice, inspiration, and friendship of many others made my time there exciting and enjoyable. This research was supported in part by the Cooperative Forest Ecosystem Research (CFER) Program and Shaubert and Tarrant Fellowships from the Department of Forest Science.

Jocelyn O'Neill has closely shared my highs and lows throughout this project, and endured many months as a "dissertation widow" as I juggled thesis, job, and fatherhood. Her encouragement, advice, and, not rarely, a joke or two, helped me to persevere. Liam Sarr provided a smile and laugh many a day when energy and enthusiasm were flagging, reminding me why I should press onward.

CONTRIBUTIONS OF AUTHORS

Chapters Two, Three, and Four are manuscripts prepared for publication with the help of Dr. David Hibbs, my thesis advisor. Under Dr. Hibbs' guidance, I planned and implemented all three studies described in this manuscript and his ideas and influence are incorporated throughout. Jeff Shatford and Rick Momsen assisted, variously, in data collection, conceptual model development, data analysis, and writing of Chapter Four.

TABLE OF CONTENTS

	<u>Page</u>
CHAPTER ONE - GENERAL INTRODUCTION	1
FACTORS INFLUENCING RIPARIAN VEGETATION DISTRIBUTION.....	2
MULTISCALE MODELS OF RIPARIAN PLANT DIVERSITY	3
REGENERATIVE DYNAMICS OF NATIVE RIPARIAN TREES	5
FIELD STUDIES AND STUDY SITE OVERVIEW	6
CHAPTER TWO - WOODY RIPARIAN PLANT DISTRIBUTIONS IN FOUR WESTERN OREGON WATERSHEDS	11
INTRODUCTION	11
STUDY OBJECTIVES	13
METHODS	13
Study Area.....	13
Field Sampling	14
Compilation of Regional Scale Variables	19
Data Analysis	20
RESULTS	23
Regional Floristic Patterns	23
Indirect Gradient Analyses.....	27
Species Associations with Climate, Topography, and Disturbance	33
DISCUSSION	38
Landscape Scale Controls on Riparian Species Distributions.....	39
Local Scale Controls on Species Distributions	41
CHAPTER THREE - MULTISCALE CONTROLS ON WOODY PLANT DIVERSITY IN WESTERN OREGON RIPARIAN FORESTS	43
INTRODUCTION	43
STUDY OBJECTIVES AND HYPOTHESES.....	44
METHODS	47
Field Sampling	47
Data Analysis	57
RESULTS	60
Statistical Summaries and Modeling Analyses	60
Multiscale Controls on Species Diversity	64
Controls on Hectare Scale Richness.....	68
DISCUSSION	73
Multiscale Controls on Species Diversity	73
CONCLUSIONS	77
CHAPTER FOUR - RIPARIAN TREE REGENERATION IN WESTERN OREGON: THE ROLES OF LIFE HISTORY, ENVIRONMENTAL GRADIENTS, AND GAP DISTURBANCE.....	79
INTRODUCTION	79
STUDY OBJECTIVES	81
METHODS	81
Identification of Functional Groups Related to Riparian Tree Regeneration.....	81

TABLE OF CONTENTS (Continued)

	<u>Page</u>
Development of the Life History / Context Model	85
Field Sampling	88
Data Analysis	95
RESULTS	97
Geographic and Topographic Patterns of Riparian Tree Regeneration.....	97
Environmental Factors Associated with Regeneration.....	102
Nurse Logs	105
Gap-Forest Comparisons.....	106
Evaluation of the Regeneration Model.....	109
DISCUSSION	110
CHAPTER FIVE - SUMMARY, MANAGEMENT IMPLICATIONS, AND CONCLUSIONS ..	114
CONTROLS ON WOODY PLANT DISTRIBUTION.....	114
CONTROLS ON WOODY PLANT DIVERSITY	117
CONTROLS ON RIPARIAN TREE REGENERATION	118
FOREST MANAGEMENT IMPLICATIONS	120
CONCLUSIONS	122
BIBLIOGRAPHY.....	123
APPENDIX	138

LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
1.1 Mean (\pm standard deviation) afternoon relative humidity for six trans-riparian transects sampled at streamside, 10 m, and 20 m from the stream in the Applegate and Alsea basins, late July to early September, 2000. All samples were collected during clear, seasonal weather.....	10
2.1. Study area and location of study watersheds and sample sites.	14
2.2 Diagram illustrating the location of: (a) the hectare plot relative to an access road and sample stream, and (b) the arrangement of subplots, sampling cells, and 40 m ² sampling plots within the hectare plot.	17
2.3. Plexus diagram based on pairwise Jaccard's analyses for the four study watersheds. Thickness of arrows indicates the degree of similarity between watershed pairs. Actual values of Jaccard's Index (C_j) are provided in parentheses.....	23
2.4. Ordination biplot of species distributional centroids based on nonmetric multidimensional scaling (NMS) axes 1 and 2 for hectare samples (n=64) in the four study watersheds. Environmental variables with Pearson's correlation coefficients > 0.32 with either axis are overlaid as vectors. Vector x and y coordinates are proportional to correlation with axes 1 and 2, respectively. Variable code definitions are provided in Table 2.2 and species names are provided in Table 2.3.	28
2.5a. Ordination biplot of species distributional centroids based on nonmetric multidimensional scaling (NMS) axes 1 and 2 for gap and forest samples (n=480) in the four study watersheds. Environmental variables with Pearson's correlation coefficients > 0.32 with either axis are overlaid as vectors. Vector x and y coordinates are proportional to correlation with axes 1 and 2, respectively. Variable codes definitions are provided in Table 2.2 and species names are provided in Table 2.3.	31
2.5b. Ordination biplot of species distributional centroids based on nonmetric multidimensional scaling (NMS) axes 1 and 3 for gap and forest samples (n=480) in the four study watersheds. Environmental variables with Pearson's correlation coefficients > 0.32 with either axis are overlaid as vectors. Vector x and y coordinates are proportional to correlation with axes 1 and 3, respectively. Variable code definitions are provided in Table 2.2 and species names are provided in Table 2.3.	32
3.1. Study area and location of study watersheds and sample sites.	48
3.2. Diagram illustrating the location of: (a) the hectare plot relative to an access road and sample stream, and (b) the arrangement of the subplots, sampling cells, and 40 m ² sampling plots within the hectare plot.....	49
3.3a,b. (a) Modeled understory light at three levels of available soil water (estimated to correspond with hillslope, midslope, and streamside topographic positions) in each of the four study watersheds. (b) Mean (+S.E.) understory light estimates based on field sampling in each watershed at streamside, midslope, and hillslope sites (n=16 per topographic position per watershed).	61
3.4 a-d. Scatterplots of predawn plant moisture stress (xylem pressure potential) in (MPa) for conifer seedlings and streamside shrubs < 2 m tall as a function of height above the stream for focal streams in each study watershed, mid-September, 2000: (a) Applegate watershed, (b) South Umpqua watershed, (c) McKenzie watershed, (d) Alsea watershed. ..	63

LIST OF FIGURES (Continued)

<u>Figure</u>	<u>Page</u>
3.5 Map illustrating spatial pattern of woody species richness across the 64 sample hectares in the Alsea, McKenzie, South Umpqua, and Applegate watersheds. Species richness is highest in the two southern watersheds and in the eastern McKenzie watershed.....	69
3.6. Relationship between modeled estimates of Gross Primary Productivity (GPP) and the gap difference (total species for 10 sampling plots in gap after subtracting total for 10 sampling plots in forest sites) in species for 24 stream in the four study watersheds. Hypothesized pattern is portrayed (EXPECTED) in comparison with field data (OBSERVED). Line of best fit for field data is from polynomial regression.	72
4.1 Ordination of riparian tree species (triangles) in two dimensional attribute space.	84
4.2 a,b.- a.) <i>Life history-context regeneration model</i> displaying optimal regeneration domains for each functional group in a two dimensional space of microclimate and light availability. The model illustrates the range of microclimates available for riparian tree regeneration in different subregions of western Oregon. b.) The model with canopy cover gradients (i.e., open, gap, forest) overlaid. See the text for further explanation and examples.....	89
4.3. Map of study area and location of study watersheds and study sites. Triangles denote major regional cities.	90
4.4. Diagram illustrating the location of: (a) the hectare plot relative to an access road and sample stream, and (b) the arrangement of the subplots, sampling cells and 40 m ² sampling plots within the hectare plot.....	92
4.5 a-f. (a-e.) Bar graphs portraying frequency (%) of sampling plots with tree regeneration for each functional group in each topographic class (left to right: streamside, terrace toeslope, hillslope) in each watershed; (f) Total species richness in each study watershed, and the proportion in each of the functional groups.....	99
4.6 a-e. Regression tree diagrams from CART analysis for each functional group. Each split is labeled with the discriminating variable and the splitting value. Placement of the variable indicates relationship: if the variable is over left leg of split, the variable is positively associated with seedling abundance; if variable is over right leg, the relationship is negative. Boxes at each terminal node contain median seedling densities/hectare and the number of samples meeting the splitting criteria for that node. See table 4.2 for variable list.	103
4.7. Percentages of seedling found on nurse logs for hardwood and conifers seedlings in each study watershed with all species weighted equally.	106

LIST OF TABLES

Table	Page
2.1. Mean (standard deviation (S.D.)) climate parameters for 16 one-hectare plots in the four study watersheds.....	15
2.2 Environmental variables used in nonmetric multidimensional scaling (NMS) with descriptions. Variables include: a) landscape scale variables used in both hectare and sampling plot scale ordinations, b) sampling plot scale variables used in the sampling plot scale ordination, and c) hectare scale summary variables used in the hectare scale ordination. The latter are mean values for all sampling plots (n=18) in the hectare, unless stated otherwise.....	22
2.3. Species encountered in riparian inventory, species codes, and frequency species was encountered in sampling plots (n=288) in each watershed (* = species recorded in hectare, but not in sampling plots.) Table is sorted so that species with highest frequency in the Applegate are at top and in the Alsea at bottom. a.) Trees, b.) Shrubs and ferns.....	24
2.4a,b. (a) Variance explained by the three NMS Axes and Pearsons correlations coefficients between each axis and the environmental variables: (a) hectare scale ordination. (b) sampling plot scale scale ordination. Variable code definitions provided in Table 2.2.	29
2.5a,b. Results of X^2 test of the null hypothesis of homogeneity in species frequency across climatic settings (the four study watersheds) and topographic positions (streamside, midslope, and hillslope sampling plots) in the riparian inventory, and gap vs. forest settings for the gap inventory. Frequencies presented for gap and forest settings are number of plots with species out of 240 gap or forest sampling plots. Tests are for all species that occurred at least 5 times in the respective dataset (n= 75 species for the riparian inventory and n = 65 for the gap/forest dataset). Topographic preference is provided for significant topographic associations. a.) Trees, b.) Shrubs and ferns.....	34
3.1 Summary of sample units for the two field inventories. Hectare plot, subplot, and sample plot locations in the riparian inventory are illustrated in Figure 3.2.	52
3.2. Environmental variables used in multiple regression analyses. Variables include: a) Landscape scale variables used in both hectare and sampling plot scale analyses, b) hectare scale summary variables used in the hectare scale analysis (mean values for all sampling plots (n=18) in the hectare, unless stated otherwise), c) sampling plot scale variables used in the sampling plot scale analysis, and d) variables used to analyze beta diversity.....	59
3.3. Mean (\pm standard deviation (S.D.)) richness of trees, shrubs, and all woody plants in each study watershed at two scales: a.) hectare scale, b.) sampling plot (alpha) scale for streamside, midslope, and hillslope topographic positions.....	65
3.4. Multivariate models selected by stepwise multiple regression for sampling plot (40 m ²) scale richness (alpha diversity) of trees, shrub, and all woody species for streamside, midslope, and hillslope topographic classes. For each model, partial coefficients of determination (R^2 values) follow order of regression equation parameters from left to right. See Table 3.2 for variable definitions.....	66

LIST OF TABLES (Continued)

Table	Page
3.5a,b. Multivariate models selected by stepwise multiple regression for a.) beta diversity, and b.) hectare scale diversity. For each model, partial coefficients of determination (R^2 values) follow order of regression equation parameters from left to right.	70
3.6 Mean tree, shrub and total species richness at sampling plot (individual gap), stream reach (total from 10 forest or gap plots at a site, approximately the hectare scale) and watershed (60 gap and forest samples) scales for the Alsea, McKenzie, South Umpqua, and Applegate watersheds. Standard deviations and results of paired one-sided t-test are provided at the stream reach scale. Statistical analyses are provided only for stream reach scale samples.	71
4.1 Riparian tree species encountered in the four study watersheds, western Oregon, with four letter species codes, and functional group membership. Life history attributes are ranked from 1 (lowest tolerance or seed size) to 10 (highest) for each species.	83
4.2. Environmental variables used in classification and regression tree (CART) analyses. Variables include: a) Landscape scale variables, b) Sampling plot scale variables.	96
4.3. Mean (+ standard deviation) seedlings per hectare for each species (arranged by functional group) and for all species for sampling plots in three topographic positions (streamside, terrace, hillslope) of each study watershed in the riparian inventory. Full species names are provided for each species code in Table 4.1.	100
4.4. Seedlings per hectare for each species are for sixty pooled gap and forest samples in each watershed. Full species names are provided for each species code in Table 4.1.	108
4.5. Percent accuracy and statistical significance for predictions of the regeneration model (Figure 4.2) for gap inventory dataset. The table lists accuracy for each functional group, all functional groups combined, and when predictions for FG4 are applied to FG3.	109

MULTISCALE CONTROLS ON WOODY RIPARIAN VEGETATION: DISTRIBUTION, DIVERSITY, AND TREE REGENERATION IN FOUR WESTERN OREGON WATERSHEDS

CHAPTER ONE - GENERAL INTRODUCTION

Riparian forests are considered essential contributors to biodiversity in the Pacific Northwest (Naiman et al. 1993, USDA and USDI 1994b), and basic information about the composition, diversity, and regenerative dynamics of these systems is needed to guide conservation and restoration. Work to date has emphasized the role of geophysical processes in structuring riparian ecosystems in the Pacific Northwest (Hawk and Zobel 1974, Fonda 1974, Grant and Swanson 1995, Fetherston et al. 1995, Swanson et al. 1998, Nakamura et al. 2000, Johnson et al. 2000) and elsewhere (Rood and Mahony 1990, Scott et al. 1996, Auble and Scott 1998). However, riparian forests show complexity at many scales, with local hydrologic and disturbance dynamics playing out on heterogeneous landscapes patterned by larger scale gradients of climate, topography, and geology (Patten 1998, Montgomery 1999). A growing body of research has suggested that such contextual factors may also be needed for an integrative understanding of riparian forest ecology in complex landscapes (Collins et al. 1981, Baker 1989, Bendix 1994, Pabst and Spies 1998, 1999, Mouw and Alaback 2002). This dissertation seeks such integration through a study of the multiscale controls on plant distribution, diversity, and regenerative dynamics in western Oregon riparian forests.

FACTORS INFLUENCING RIPARIAN VEGETATION DISTRIBUTION

“..wild, no less than cultivated trees, each have their own positions; some love wet and marshy ground, such as black poplar, and those in general that grow by rivers; some love exposed and sunny positions, some prefer a shady place..”

---Theophrastus, 300 B.C.

(excerpted from Wells and Anzinger 2001, p 31)

When beginning a regional study of vegetation, perhaps the most fundamental question to ask is: Why do plant species occur where they do? This might seem a rather straightforward question for an exploration of riparian vegetation, that by definition occurs near rivers and streams. Yet even this closely defined landscape and its vegetation reflect influences that span multiple spatial and temporal scales (Baker 1989, Bendix 1994, Dixon et al. 2002). The great variety in riparian vegetation described in the western United States (Fonda 1974, Hawk and Zobel 1974, Baker 1989, Bendix 1994, Minore and Weatherly 1994, Patten 1998, Pabst and Spies 1998, 1999, Dykaar and Wigington 2000, Nierenberg and Hibbs 2000, Hibbs and Bower 2001, Mouw and Alaback 2002) is testimony to the importance of these influences. It also highlights the need for understanding how riparian vegetation changes across larger landscapes and what factors control this change.

Riparian ecologists have often emphasized local associations between riparian plants and specific landforms, hydrologic conditions, or seral settings (Hack and Goodlet 1960, Fonda 1974, Hawk and Zobel 1974, Harris 1987). This has led to a rather discrete perspective of riparian plant distributions, where local disturbances and associated landforms are believed to generate a patch mosaic, creating the emergent landscape pattern (Malanson 1993). This contrasts with a continuum view developed in studies of upland communities, where species have been proposed to be individualistically and continuously distributed along environmental gradients

(Gleason 1926, Whittaker 1956, 1960, Vankat 1982, Austin and Smith 1989). An emerging realization that riparian forests form part of a landscape continuum, and that they show important regional variation (Pabst and Spies 1998, 1999, Patten 1998), has heightened the importance of complementing the mosaic paradigm with gradient-based and multiscale perspectives of species distributions. I explore these principles and investigate the roles of local and landscape scale controls on riparian plant distributions in Chapter Two of this dissertation.

MULTISCALE MODELS OF RIPARIAN PLANT DIVERSITY

Riparian forests are believed to be among the most floristically diverse terrestrial ecosystems (Gregory et al. 1991, Naiman et al. 1993, Mouw and Alaback 2002), but ecologists are only beginning to unravel the sources of this complexity. Riparian vegetation is shaped by multiscale factors (Baker 1989, Bendix 1994, Fetherston et al. 1995, Pabst and Spies 1998, Dykaar and Wigington 2000, Johnson et al. 2000, Wimberly and Spies 2001, Dixon et al. 2002), which undoubtedly also affect the diversity of species present. Conserving riparian plant diversity will require a better understanding of the relative importance of these factors in maintaining diversity, and, equally important, how they interact.

In upland environments, a growing body of theoretical and empirical work has sought either to contrast or integrate how local and landscape or regional scale factors influence species diversity (Ricklefs 1987, Caley and Schluter 1997, Cornell 1999, Huston 1999a, Sarr et al. in press). Most field studies and biodiversity theory have focused on the effects of local controls such as soil resource or light availability, competition, and disturbance dynamics on floristic diversity (Grime 1973, Huston 1979, 1999a, Tilman 1982, 1987, Stevens and Carson 2002). Larger scale studies have illustrated how historical or climatic factors may also act to constrain diversity (Ricklefs 1987, Kleidon and Mooney 2000).

All these factors probably influence riparian vegetation, yet relatively few studies have explored plant diversity in riparian settings (but see Pollock et al. 1998, Nilsson et al. 1989, Mouw and Alaback 2002). Riparian disturbance processes are believed to limit competitive exclusion in the riparian zone, and they have been linked to nonequilibrium models of species diversity (e.g., Connell 1978, Huston 1979) in several geographic settings (Nilsson et al. 1989, Pollock et al. 1998). Local factors maintaining environmental heterogeneity also appear important for floristic diversity in upland (Huston 1994, Tilman 1994) and riparian plant communities (Gould and Walker 1997). In riparian forests, heterogeneity is expressed at the smallest scales by variation in geomorphology, substrate, or light at individual sites, and by the dynamic mosaic of disturbance, light, soil moisture, or soil drainage conditions on floodplains (Hack and Goodlet 1960, Hawk and Zobel 1974, Fonda 1974, Duncan 1993, Harris 1987, Sakai et al. 1999). In addition, environmental gradients, such as the changes in light availability, substrate characteristics, and moisture availability from streamsid es to hillslopes probably influence species turnover (beta diversity *sensu* Whittaker 1960, Wilson and Shmida 1984) across the riparian zone.

A more complete understanding of species diversity in riparian forests would complement these local observations with information about how riparian forests change across larger landscapes (see Bendix 1994). It is unclear, for example, how strongly landscape scale controls on plant distribution, such as climate, interact with or regulate local structures and processes. Are landscape scale controls primary or secondary influences? Do they influence species directly through physiological mechanisms? Or do they act indirectly, by controlling the competitive dynamics and gradient structure of the riparian ecosystem? My central goal in this dissertation was to develop a better understanding of the multiscale relationships between the environment and woody plant diversity in riparian forests. Chapter Three is an exploration of these relationships.

REGENERATIVE DYNAMICS OF NATIVE RIPARIAN TREES

Despite a regional emphasis on riparian conservation and restoration, natural regenerative dynamics for many species of riparian trees are still poorly understood in the Pacific Northwest. The few existing studies have demonstrated important differences in regeneration among tree taxa and environmental settings (Minore and Weatherly 1994, Hibbs and Giordano 1996, Pabst and Spies 1999). Near stream margins, flood abrasion and seasonally anaerobic soils favor establishment of species with rapid juvenile growth, flexible stems, and flood tolerance, whereas on higher terraces, drought and shade tolerance become more important. Longitudinal changes along river corridors also cause shifts in vegetation composition and regeneration pattern (Hupp 1986, Minore and Weatherly 1994, Tabacchi et al. 1996, Pabst and Spies 1999). As a result, riparian forests diverge in composition and structure from upland forests as stream size increases (Hupp 1986). These intra-riparian gradients, in turn, are nested within larger geographic gradients (Pabst and Spies 1999). Nurse logs form another facet of the regeneration environment for Pacific Northwest trees (Harmon and Franklin 1989), and prior riparian research suggests important geographic variation in the function of logs as establishment sites (Hibbs and Giordano 1996, Pabst and Spies 1999). Further empirical study is needed to better understand the effects of species and environmental context on regeneration dynamics in western Oregon riparian forests.

The host of site and species interactions complicates the task of predicting where planted or naturally seeded trees will best establish. Models of tree regeneration have the potential to clarify mechanisms and predict natural patterns of regeneration across species and sites. Most models of forest dynamics have interpreted regeneration strategies as evolutionary responses to the spatial and temporal variability in conditions caused by disturbance (Grubb 1977, Pickett and White 1985, Whitmore 1989, Veblen 1992). Other models have stressed the role of spatial gradients in resource availability and its importance in selecting for distinct

growth strategies (Grime 1977). In riparian forests of western Oregon, disturbance and environmental gradients probably both influence riparian regeneration, given the regional heterogeneity in climate, topography, soils, and disturbance. Models that link life history traits with local and regional shifts in resource availability may provide a means to better predict regeneration dynamics across species and settings. I develop a model of riparian tree regeneration in Chapter Four of this dissertation that integrates life history characteristics with predicted shifts in environmental conditions caused by climate and disturbance. I evaluate the model using riparian tree regeneration data from four western Oregon watersheds.

FIELD STUDIES AND STUDY SITE OVERVIEW

This dissertation describes two closely related field studies conducted in western Oregon in 1999 and 2000. I selected four watersheds for study because they span the range of climatic settings at low elevations in western Oregon, and because they each contain substantial area administered by the USDI Bureau of Land Management (BLM). The four focal study watersheds (from south to north) were the Applegate, South Umpqua, McKenzie, and Alsea watersheds. All sampling was conducted in areas of low to moderate elevation with approximately similar mean annual temperature, but precipitation and seasonal temperature regimes are distinct in each study watershed. This research was funded under the Cooperative Forest Ecosystem Research (CFER) Program with the goal of providing a better understanding of local and regional variation in woody plant composition, diversity, and tree regeneration along low order streams of BLM lands in western Oregon.

The Applegate watershed drains the north central slope of the eastern Siskiyou Mountains in southwest Oregon and extreme northern California. The watershed is characterized by ancient bedrock, with folded and metamorphosed parent materials and complex soils, including serpentine. The watershed has rugged

topography with elevations ranging from over 2100 m on Wagner Butte at the eastern edge to 260 m at the confluence with the Rogue River west of Grants Pass, Oregon. Major tributaries of the Applegate River all drain north from the Siskiyou crest and include the Little Applegate River, Williams Creek, and Thompson Creek. All field sampling was conducting in tributaries above the Williams Creek confluence. The blocking effect of Grayback Mountain at the western margin of the watershed limits winter precipitation and ingress of cool maritime air in summer, creating a distinct climatic and vegetation province where many species that are widespread in wetter climates are absent or rare (see Waring 1969). However, the watershed harbors a rich and complex flora with many relictual species and a number of specially designated botanical areas. Forest vegetation is dominated by *Pseudotsuga menziesii* (Mirbel) Franco, but many other woody species are locally important associates, including *Calodendrus decurrens* (Torr.) Florin., *Pinus lambertiana* Dougl., *Arbutus menziesii* Pursh., *Quercus chrysolepis* Liebm., and *Acer macrophyllum* Pursh. In the wetter western watershed, *Chamaecyparis lawsoniana* (A. Murr.) Parl. is abundant on floodplains with *Alnus rubra* Bong., and *Acer circinatum* Pursh. Eastward in the watershed many mesophytic species drop out and more drought tolerant species appear, including *Quercus kelloggii* Newberry, *Q. garryana* Dougl., *Pinus ponderosa* Dougl., and, near streams, *Alnus rhombifolia* Nutt.

The South Umpqua River drains the western flank of the southern Cascades from just northwest of Crater Lake National Park to its confluence with the North Umpqua River. Elevations in the watershed range from approximately 2046 m on Fish Mountain on the Rogue/Umpqua divide to 120 m at the confluence with the North Umpqua River near Roseburg. The geology of the region ranges from Klamath terranes at the westernmost sites, to volcanic extrusives in the upper watershed (Orr and Orr 1999). Primary tributaries of the South Umpqua River include Cow Creek and Jackson Creek. I sampled riparian vegetation in the upper watershed primarily above the town of Tiller, but also at the head of the Cow Creek

subdrainage. The vegetation is primarily mixed conifer forest at lower elevations with *Tsuga heterophylla* (Raf.) Sarg. and *Thuja plicata* Donn locally dominant on floodplains and cooler aspects and with xerophytic species such as *P. lambertiana*, *C. decurrens* occurring on convex slopes or warmer aspects. A number of species that occur in the Applegate watershed, including *A. menziesii*, *Q. kelloggii*, *P. ponderosa*, and *A. rhombifolia* are also present, but much less abundant. In general, the watershed combines many of the species that are widespread in northwest Oregon with distinctive southern species.

The McKenzie watershed drains the western slope of the Oregon Cascades. Elevations in the watershed range from over 3100 m on South Sister just over 100 m where the McKenzie joins the Willamette River north of Eugene. Geology of the watershed ranges from the volcanic extrusive platform of the High Cascades to the older, more deeply eroded volcanics of the Western Cascades. The entire upper watershed was affected by Pleistocene mountain glaciation and glacial features are prominent. Major tributary drainages include the Blue River watershed entering from the north and the South Fork of the McKenzie that enters from the south. Vegetation of the watershed is well studied (Hawk and Zobel 1974, Dyrness et al. 1974, Zobel et al. 1976) and is primarily dominated by mature and old growth *Pseudotsuga-Tsuga* forest with *T. plicata* also abundant. Southern species, such as *C. decurrens* occur occasionally, primarily on convex landforms and southern or western exposures. Streamsides are often dominated by *A. rubra* on lower order streams, with *Populus trichocarpa* T. & G. dominating on the main stem of the McKenzie River.

The Alsea watershed drains the western slope of the Oregon Coast Range and encompasses elevations from 1245 m at the summit of Mary's Peak to sea level. Geology is characterized by uplifted ocean floor sediment with occasional basalt intrusions that form prominent peaks. Major tributaries to the Alsea River include Parker Creek, Drift Creek, and Canal Creek. Vegetation of the Alsea watershed is dominated by second growth to mature *P. menziesii* forest with occasional stands of

T. heterophylla. *A. rubra* is often dominant in disturbed areas. *A. macrophyllum* and *F. latifolia* are also common, with the latter becoming more important in the drier upper watershed. *A. rubra* is typically dominant or codominant in riparian forests, often with a dense understory of the clonal shrub *Rubus spectabilis* Pursh. The latter species often forms large shrub fields where trees are rare or absent (Pabst and Spies 1998, Nierenberg and Hibbs 2000). Occasional conifer-dominated stands often have a mixture of *P. menziesii*, *T. heterophylla*, and *T. plicata*. Within 10 km of the coast, where marine stratus and fogs attenuate solar radiation and temperature for most of the summer, a number of distinctive species occur. *Picea sitchensis* (Bong) Carr. is often the dominant tree in this coastal fog zone, with *P. menziesii* much less abundant than just a few km inland (Franklin and Dyrness 1988, Wimberly and Spies 2001). The shrubs *Menziesia ferruginea* Smith, and *Vaccinium ovatum* Pursh are also much more common in the coastal fog zone than elsewhere.

I explored the role of the sharp climate gradient represented by the four watersheds in shaping composition and dynamics of woody riparian vegetation along otherwise similar streams. Field measurements of relative humidity at opposite ends of the gradient demonstrate that regional climate differences coincide with important differences in microclimate in local riparian forest environments (Figure 1.1).

The climate gradient provided an excellent regional setting in which to evaluate relationships between climate, riparian gradient structure, and vegetation, and to contrast them with effects of local factors. The three succeeding chapters explore these relationships. Chapter Two analyzes woody species distributions across the gradient. Chapter Three explores local and landscape scale controls on woody plant diversity at several scales and evaluate hypotheses about the strength and interrelationships among these controls. Chapter Four develops a tree regeneration model based on published life history traits and expected shifts in the regeneration environment associated with local and regional gradients. In the closing chapter (Chapter Five), I summarize key findings from the three field studies and discuss their implications for regional riparian forest management.

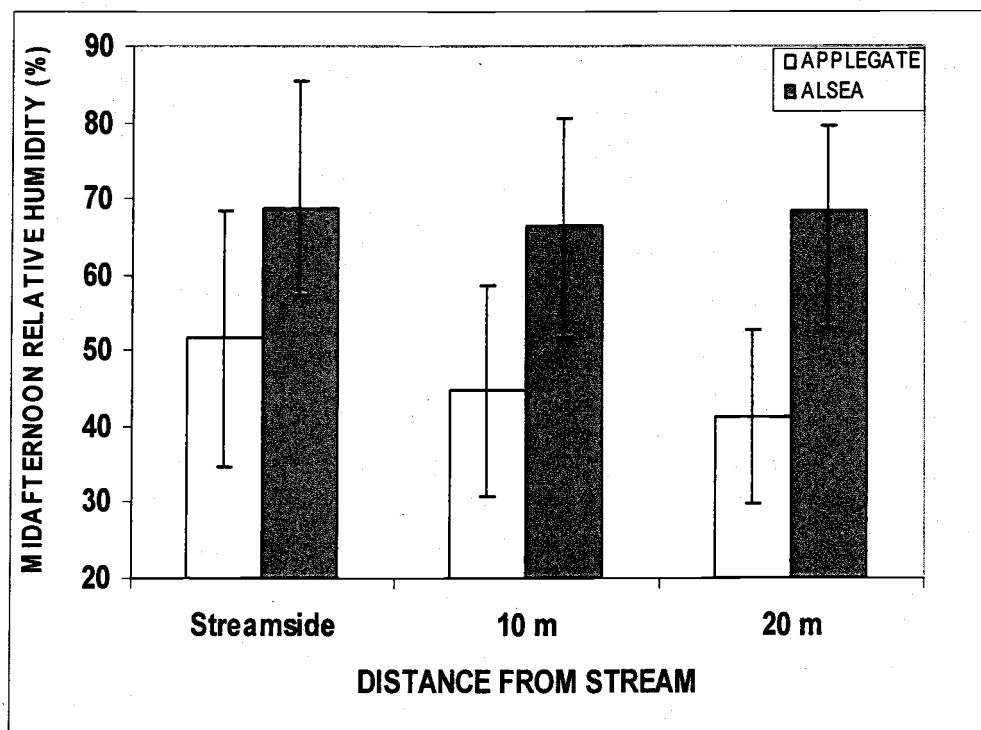


Figure 1.1 Mean (\pm standard deviation) afternoon relative humidity for trans-riparian transects sampled ($n = 6$) at streamside, 10 m, and 20 m from the stream in the Applegate and Alsea watersheds, late July to early September, 2000. All samples were collected during clear, seasonal weather.

CHAPTER TWO - WOODY RIPARIAN PLANT DISTRIBUTIONS IN FOUR WESTERN OREGON WATERSHEDS

INTRODUCTION

The riparian vegetation composition in any region reflects landscape and local scale influences (Baker 1989, Bendix 1994, Dixon et al. 2002), yet the majority of riparian field studies have focused only on local patterns and mechanisms (Fonda 1974, Hawk and Zobel 1974, Harris 1987, Johnson 1994, Robertson and Augsberger 1999, Dykaar and Wigington 2000, Mouw and Alaback 2002). In the western United States, great variation in riparian vegetation structure and composition (Fonda 1974, Hawk and Zobel 1974, Baker 1989, Bendix 1994, Minore and Weatherly 1994, Patten 1998, Pabst and Spies 1998, 1999, Dykaar and Wigington 2000, Nierenberg and Hibbs 2000, Hibbs and Bower 2001, Mouw and Alaback 2002) highlights the need for understanding how riparian vegetation changes across larger landscapes and what factors control this change. This study explores multiscale controls on riparian plant species distributions in western Oregon.

The few existing landscape scale studies suggest climate may be an important driver of riparian plant species distributions (Collins et al. 1981, Alcaraz et al. 1997). Climate may influence the structure of riparian moisture gradients, the area of the floodplain that has anaerobic soils, riparian microclimates, and the structure and composition of vegetation (Patten 1998, Pabst and Spies 1998, 1999). The position of the site within the watershed (i.e., stream order) is also important (Hupp 1986, Baker 1989, Bendix 1994).

At the local scale, hydrologic and geomorphic processes play a major role in shaping the riparian environment (Gregory et al. 1991, Pollock et al. 1998, Naiman et al. 2000). Consequently, riparian ecologists have often interpreted riparian vegetation composition as a somewhat predictable outcome of specific hydrologic regimes, geomorphic structures, or successional states (Hack and Goodlet 1960,

Fonda 1974, Hawk and Zobel 1974, Hupp and Osterkamp 1985, Harris 1987, Fetherston et al. 1995, Pabst and Spies 1998, Robertson and Augsberger 1999). However, it is by no means certain that all plant species in a riparian forest are governed exclusively, or even primarily, by fluvial processes and landforms. Riparian forests are influenced by many of the same disturbances as upland forests. Fine-scale gap disturbances originating from a variety of sources (e.g., windthrow, tree snap, pathogens, and landslides) have been demonstrated to influence local species distributions in *Quercus-Ulmus* riparian forests in Japan (Sakai et al. 1999), and are probably important in many riparian forest landscapes. Larger scale upland disturbances, such as fire, probably also have important effects on riparian plant distributions.

Biotic processes form additional controls on landscape scale vegetation patterns as well as local scale riparian species distributions. Waring et al. (2002), presenting data on light availability and woody plant richness in upland sites across Oregon, speculated that increased vegetation density and decreased understory light from dry to wet climates of western Oregon excludes species from the wettest forests. It is likely that these general geographic patterns affect riparian forest plant distributions as well. Riparian field studies in the Pacific Northwest have suggested that interspecific competition plays an important role in controlling plant distributions in riparian forests (Pabst and Spies 1998, Nierenberg and Hibbs 2000). In particular, several authors have noted the singularly important influences of *Rubus spectabilis* Pursh, a clonal shrub that grows 2 to 3.5 meters tall and forms dense, persistent thickets, on riparian vegetation and tree seedling establishment in the Oregon Coast Range (Tappeiner et al. 1991, Minore and Weatherly 1994, Pabst and Spies 1998). Tappeiner et al. (1991) explored the competitive mechanisms whereby *R. spectabilis* competitively excludes other species. Rapid clonal growth, thickets of regenerating aerial stems from long-lived underground rhizomes, and early leaf out in spring were traits highlighted as allowing effective competition for space and resources above and below ground (Tappeiner et al. 1991).

STUDY OBJECTIVES

In this study, our objectives were twofold: (1) describe floristic variation in riparian forests of western Oregon, and (2) understand better the drivers of this variation. To address these objectives, we analyzed floristic and environmental data from two related riparian field studies in four watersheds of western Oregon, asking two research questions:

- (1) What are the major floristic elements in riparian forests of western Oregon?*
- (2) How do landscape scale and local scale environmental factors influence riparian species distributions at multiple scales?*

METHODS

Study Area

In western Oregon, a steep climate gradient extends from the southern interior towards the north and west, with annual precipitation increasing from approximately 600 mm in the eastern Siskiyou Mountains to >2500 mm in the western Coast Range (Franklin and Dyrness 1988). During the summer, southern interior areas are warmer, drier, and sunnier than northern and coastal areas. Coniferous forests dominate the study area, with broadleaved evergreen and deciduous hardwoods forming important secondary components in the driest and wettest climates, respectively (Franklin and Dyrness 1988).

In the summers of 1999 and 2000, we sampled riparian vegetation in four watersheds of western Oregon: (1) the Applegate in the eastern Siskiyou Mountains, (2) the South Umpqua in the southern Cascades; (3) the McKenzie in the central western Cascades, and (4) the Alsea in the western Coast Range (Figure 2.1). Sampling was conducted in low to moderate elevation areas of roughly similar mean

annual temperature (9-10.5 ° Celsius), but annual precipitation and precipitation days increase from south to north, while summer temperatures and vapor pressure deficits decline (Table 2.1).

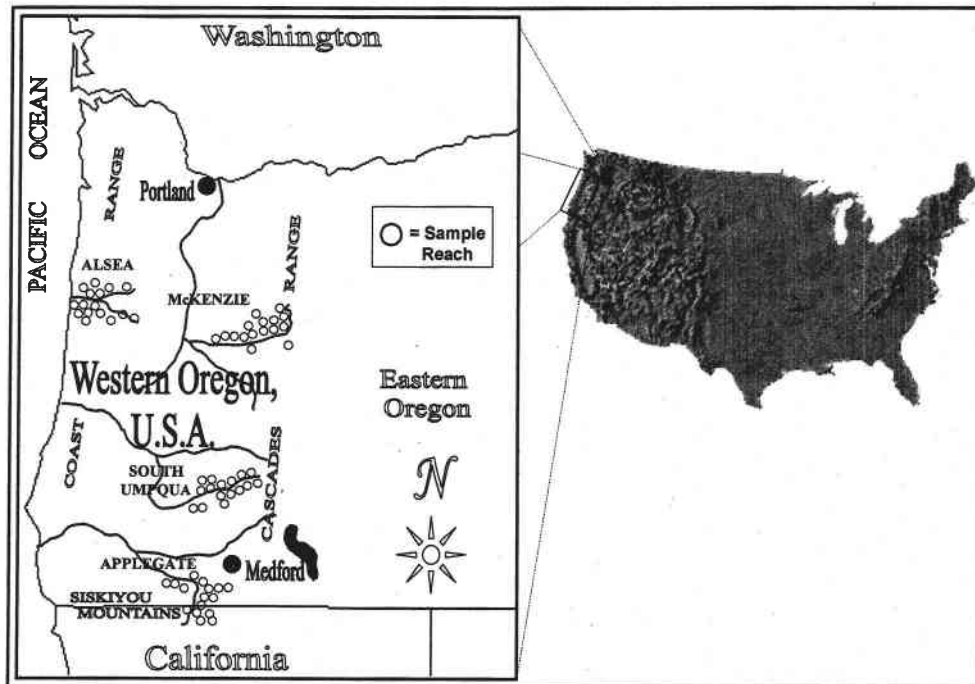


Figure 2.1. Study area and location of study watersheds and sample reaches. Dark circles signify major cities.

Field Sampling

Within these four watersheds, we sampled woody riparian vegetation in two related field studies: (a) a broad riparian inventory and (b) a gap study that used paired comparisons of forest gaps and forest interiors.

Riparian Inventory

From June to September 1999, we sampled vegetation and environmental characteristics along sixteen streams selected randomly from a population of 1st

Table 2.1. Mean (standard deviation (S.D.)) climate parameters for 16 one-hectare plots in the four study watersheds.

CLIMATE PARAMETERS	STUDY WATERSHEDS							
	Applegate		South Umpqua		McKenzie		Alsea	
	Mean	(S.D.)	Mean	(S.D.)	Mean	(S.D.)	Mean	(S.D.)
Mean Annual Temperature (°C)	10.0	(0.7)	10.2	(0.6)	9.1	(0.6)	10.5	(0.5)
Mean Annual Precipitation (mm)	1000	(157)	1257	(115)	1871	(197)	2116	(118)
Mean Annual Precipitation Days (days with > 0.254 mm precipitation)	98.5	(0.8)	129.9	(4.1)	150.7	(5.8)	157.9	(2.8)
July Maximum Temperature (°C)	27.8	(1.4)	27.2	(0.8)	24.8	(0.9)	22.1	(1.1)
January Minimum Temperature (°C)	-1.5	(0.5)	-1.4	(0.5)	-2.2	(0.7)	2.2	(0.9)
Growing Degree Days (base 0.0 °C)	3750	(263)	3672	(189)	3140	(237)	3961	(117)
Daytime Mean Vapor Pressure Deficit (June-Sept. (mb))	14.7	(1.2)	14.0	(0.9)	11.8	(0.9)	8.6	(1.2)

through 5th order stream reaches in each of the four study watersheds. Stream order and watershed area were determined for each stream at the sample reach from USGS

1:24,000 topographic quadrangle maps. For each watershed, we interviewed staff at the appropriate land management agency (USDA Forest Service or USDI Bureau of Land Management) to determine management histories of each potential sample reach. We then confined field sampling to stream reaches that had not had timber harvest or other management within the last 30 years and which occurred within 1 hour hiking distance (3-4 km) from an access road or trail. In each watershed, this yielded 30-50 potential reaches. Sample reaches were assigned numbers and sixteen numbers were selected at random for field sampling sites in each watershed (64 total). All plots were placed at least 50 meters upstream or downstream from a road or trail crossing and then a random distance from zero to 200 m further upstream or downstream (Figure 2.2). Although the distribution of stream orders differed substantially between the watersheds, most sample streams selected in each (56 % – 94%) were second or third order streams.

At each sample reach, we established a plot that straddled the stream and was 200 m long by 50 m wide (25 m on each side of stream), not including the stream channel, thereby encompassing a hectare of riparian forest habitat. We will refer to this plot as the hectare plot. All distances were slope distances measured along the ground surface with a fiberglass tape.

We established six pairs of 25 x 33.3 m subplots (thus 12 subplots in the whole hectare plot) with the 33.3 m side parallel to the stream (Figure 2.2). We randomly selected one subplot of each pair for sampling vegetation and environmental characteristics. We divided the subplot to produce three contiguous 8 x 33.3 m sampling cells at increasing distances from the stream edge. Data were collected in 4 m x 10 m (40 m²) sampling plots arrayed with the long side parallel to the stream. We randomly placed a sampling plot in each selected sampling cell.

Along these mountain streams, the three sampling cells usually corresponded with a horizontal and vertical gradient from (1) streamside bars to (2) midslopes/flood plain terraces and (3) lower hillslopes. Although the placement of plots varied somewhat with the morphology of the valley floor along a particular

stream, we will refer to sampling plots from the three topographic positions as (1) streamside, (2) midslope, and (3) hillslope plots.

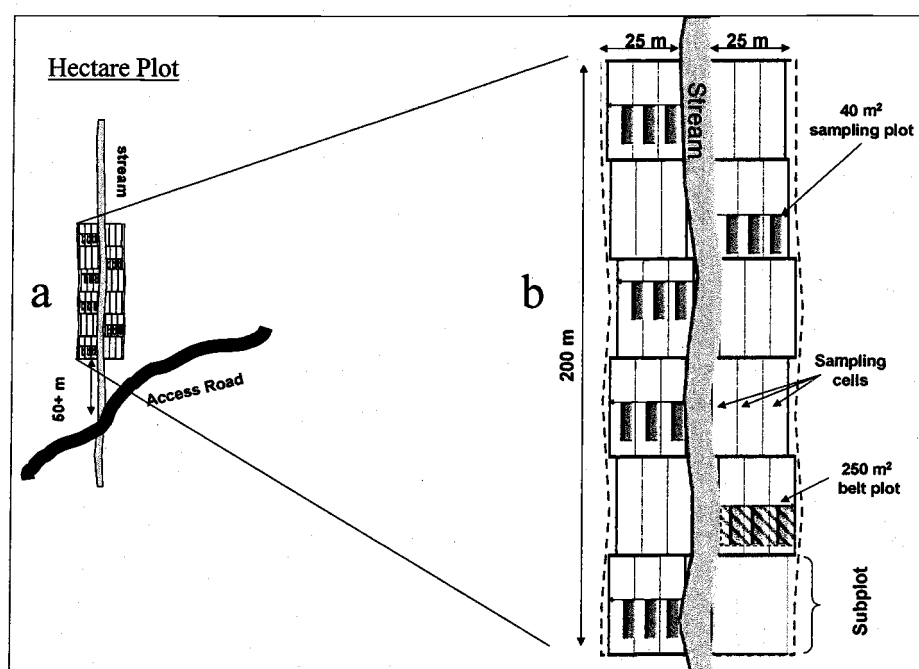


Figure 2.2 Diagram illustrating the location of: (a) the hectare plot relative to an access road and sample stream, and (b) the arrangement of subplots, sampling cells, and 40 m² sampling plots within the hectare plot.

Vegetation and environmental characteristics were collected within each sampling plot. Presence of all woody species was noted, ground distance from the plot center to the current (low flow) water's edge was recorded, and slope in degrees from the plot center to the stream edge was estimated using a clinometer held at 1 meter above the ground. Overstory cover was an ocular estimate of tree cover seen through a 20 cm diameter ring held vertically at arms length (ca. 45 cm). Total cover was estimated by applying the same method with the observer seated and included any shrub layers greater than 1.2 m above the ground in addition to overstory cover.

We determined the number of geomorphic units occurring in each sampling plot using a key to geomorphic units we developed in the field. Soil characteristics

were determined by digging a 30 cm soil pit in the middle of each sampling plot. Litter depth, and, where a bedrock layer was encountered, depth to bedrock, were measured in centimeters. If bedrock was not encountered in the top 30 cm, soil depth was recorded as 35 cm.

We also recorded two indices of disturbance in each sampling plot. An index of fluvial scouring was recorded as the proportion of each sampling plot that was visibly affected by fluvial activity, including obvious signs of fluvial erosion or deposition or flow channels. In a similar way, we recorded presence of animal herbivory by noting the proportion of the sampling plot with browsing of shrubs or trees evident. In both cases, index scores were: (1) disturbance noted in 0-20 percent of sampling plot, (2) 20-40 percent, (3) 40-60 percent, (4) 60-80 percent, and (5) 80-100 percent.

Gap Study

In summer 2000, we revisited 24 sample reaches from the 1999 inventory, 6 from each study watershed, to sample vegetation in natural forest gaps caused by tree mortality, tree bole or branch snap, fluvial scouring, or hillslope failure. Since we noted considerable east to west variation in the riparian forests of each watershed, we stratified our sampling to select randomly two streams each in the western-most, middle, and eastern-most sections of each study watershed. Beginning at the location of the 1999 hectare plot, we censused the first 10 gaps we encountered along each stream. Naturally occurring gaps ranged in area from 12m^2 to over 2000m^2 with the majority between 100m^2 and 500m^2 . In most cases, these gaps were contained within the original hectare plot, but we occasionally searched a slightly longer section of stream (up to 300 m) to locate ten gaps. We included gaps from streamside, terrace, and hillslope locations on both sides of a stream. In all, we collected 240 gap samples, 60 in each watershed. Within each gap, we randomly located a 40m^2 circular

sampling plot and collected vegetation and environmental data as described for the riparian inventory above.

We prepared a matching dataset of 240 forested sampling plots for the same 24 streams by subsampling from the riparian inventory dataset. First, we sorted all 18 sampling plots at each stream by distance classes in the riparian inventory, yielding six potential sampling plots in each class. Next, we selected the three sites with highest overstory cover in each of the three distance classes. We then randomly selected another plot from among the next densest of the three distance classes to yield a total of ten forest samples for each stream. Finally, we combined this dataset with the samples from the gap inventory to yield a gap-forest dataset with 480 sampling plots evenly split between gap and forest environments at the 24 streams.

Compilation of Regional Scale Variables

Because most of the climatic temperature and moisture variables we reviewed were strongly intercorrelated, we used only two as explanatory variables (Table 2.2). We used annual growing degree days (base 0° C, GDDTOT) as an estimate of energy available for phenological development in the growing season. GDDTOT was derived for each hectare plot from mapped climate surfaces generated by the DAYMET model (Thornton et al. 1997). We selected vapor pressure deficit in summer (VPDSUM) as an index of climatic moisture stress that was independent of the variation in subsurface water within the riparian zone. We calculated mean afternoon vapor pressure deficit for June through September from minimum and maximum temperature data at each hectare using the equations of Running et al. (1987).

To describe the local environmental conditions in each hectare plot, we averaged topographic and vegetation data for all the sampling plots within the hectare, and we calculated the topographic range in meters from the highest to the lowest sampling plot in the hectare (Table 2.2). Because clonal shrubs, especially *Rubus spectabilis*, are believed to strongly govern local species distributions (Pabst and Spies

1998), we summed the cover of all clonal species in each sampling plot and averaged these for each hectare. We also included *R. spectabilis* cover as a distinct analytical variable at both scales, since the literature (Minore and Weatherly 1994, Pabst and Spies 1998, Neirenberg and Hibbs 2000) and our initial field observations suggested that it was indeed an important influence on local plant distributions where it was abundant.

Data Analysis

Watershed Scale Comparisons

To view broad floristic patterns, we compiled species lists for each watershed from the riparian inventory (Table 2.3), and we calculated species similarity between watersheds using Jaccard's Index of Similarity (Magurran 1988):

$$(1) C_j = j / (a + b - j)$$

Where j = the number of species common to both watersheds, a = the number of species in watershed A, and b = the number of species in watershed B. Index values can range from 1 indicating identical composition to 0 indicating that the two locations have no species in common.

Indirect Gradient Analyses

We performed indirect gradient analysis using nonmetric multidimensional scaling (NMS) (Kruskal 1964, Mather 1976) in the vegetation analysis package PC-ORD (McCune and Mefford 1999) to relate variation in species composition to environmental characteristics. We conducted ordination analyses at two scales, one for our hectare scale data set and another for our sampling plot scale data set from

gap and forest environments. We used presence-absence data for all tree and shrub species that occurred at least 5 times in the data set. We ran NMS with 40 iterations using the real data and tested the result with 50 Monte Carlo simulation runs. We performed correlation analyses between environmental variables in Table 2.2 and the NMS ordination axes to identify the strongest correlates with vegetation variation, and we used the Sorenson distance function to compare variation in the original gradient space with variation in the ordination space.

We used the hectare scale analysis to evaluate the correlates of species pools at each stream reach, which each contained a roughly similar suite of local topographic and disturbance environments. To better understand local scale species distributions, we used our second dataset of 480 gap and forest sampling plots. From this sampling plot scale dataset, we explicitly compared the value of among-hectare variables and within-hectare variables in interpreting local species distributions.

Statistical tests of Habitat Associations

We tested for significant habitat associations of individual species using nonparametric X^2 analyses in the statistical package SPLUS (Mathsoft, Inc. 1988-2000). We used frequency data from our riparian inventory to test the associations of species with our study watersheds that we interpreted as distinct climatic settings and with topographic positions, and we used the gap forest data set to evaluate disturbance associations of species. In all cases we tested the null hypothesis that species frequencies were homogeneous among the four watersheds (3 d.f.), three topographic positions (2 d.f.), and gap versus forest settings (1 d.f.).

Table 2.2 Environmental variables used in nonmetric multidimensional scaling (NMS) with descriptions. Variables include: a) landscape scale variables used in both hectare and sampling plot scale ordinations, b) sampling plot scale variables used in the sampling plot scale ordination, and c) hectare scale summary variables used in the hectare scale ordination. The latter are mean values for all sampling plots (n=18) in the hectare, unless stated otherwise.

a) LANDSCAPE SCALE	
VARIABLES	VARIABLE DEFINITIONS
GDDTOT	GROWING DEGREE DAYS (0 ° C BASE)
VPDSUM	MEAN VAPOR PRESSURE DEFICIT JUNE-SEPTEMBER (mb)
LOGWA	LOGARITHM OF WATERSHED AREA (ha) ABOVE HECTARE SITE
STRMORD	STRAHLER STREAM ORDER AT HECTARE SITE
b) SAMPLING PLOT SCALE	
VARIABLES	
BROWSE	UNGULATE BROWSING (ORDINAL 1-5 SCALE)
CLONAL	CLONAL SHRUB COVER (%)
CONCOVER	PERCENT CONIFER COVER IN CANOPY LAYER
GAP	BINARY VARIABLE (1= GAP, 0= FOREST)
GEOM	GEOMORPHIC UNITS IN SAMPLING PLOT
HAS	SAMPLING PLOT HEIGHT ABOVE STREAM (m)
LDEPTH	LITTER DEPTH (cm)
OCOV	OVERSTORY COVER (%)
ROCK	EXPOSED ROCK COVER (%)
RUSP	<i>Rubus spectabilis</i> COVER (%)
SCOUR	FLUVIAL SCOURING (ORDINAL 1-5 SCALE)
SDEPTH	SOIL DEPTH (cm)
TCOV	TOTAL FOLIAR COVER (%)
c) HECTARE SCALE	
VARIABLES	
CLONAL	CLONAL SHRUB COVER (%)
CONCOVER	CONIFER COVER (%)
GEOM	GEOMORPHIC UNITS IN SAMPLING PLOTS
LDEPTH	LITTER DEPTH (cm)
OCOV	OVERSTORY COVER (%)
ROCK	EXPOSED ROCK COVER (%)
RUSP	<i>Rubus spectabilis</i> COVER (%)
SCOUR	FLUVIAL SCOURING (ORDINAL 1-5 SCALE)
SDEPTH	SOIL DEPTH (cm)
TCOV	TOTAL FOLIAR COVER (%)
TOPOGRAPHY	TOPOGRAPHIC RANGE IN HECTARE PLOT (m)

RESULTS

Regional Floristic Patterns

Species recorded in each watershed are listed in Table 2.3. A plexus diagram based on Jaccard's analysis of species overlap between watershed pairs illustrates the broad floristic relationships among watersheds (Figure 2.3). Samples from the Alsea and Applegate watersheds, at opposite ends of the climate gradient, had many distinctive species and the lowest overlap ($C_j = 0.36$). The two Cascade watersheds had the highest species similarity ($C_j = 0.70$). Although species overlap was moderate in most watershed comparisons, patterns of species similarity suggest that the four watersheds harbor three substantive floristic elements: (1) a coastal element; (2) a Cascades element, and (3) a Klamath element, each with a number of characteristic species.

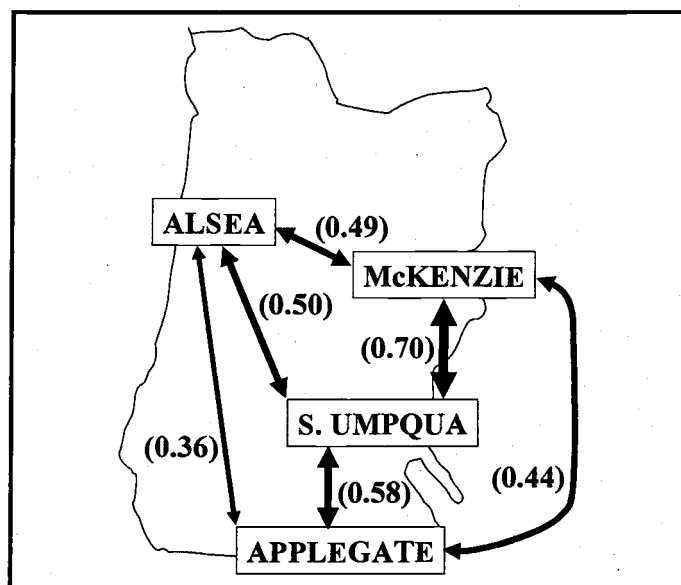


Figure 2.3. Plexus diagram based on pairwise Jaccard's analyses for the four study watersheds. Thickness of arrows indicates the degree of similarity between watershed pairs. Actual values of Jaccard's Index (C_j) are provided in parentheses.

Table 2.3. Species encountered in riparian inventory, species codes, and frequency species was encountered in sampling plots (n=288) in each watershed (* = species recorded in hectare, but not in sampling plots.) Table is sorted so that species with highest frequency in the Applegate are at top and in the Alsea at bottom. a.) Trees, b.) Shrubs and ferns.

a) Tree Species

SPECIES NAME	SPECIES CODE	FREQUENCY (% of Sampling Plots)			
		STUDY WATERSHED			
		Applegate	South Umpqua	McKenzie	Alsea
<i>Pseudotsuga menziesii</i> (Mirbel) Franco	PSME	68.4	35.8	32.3	12.8
<i>Quercus chrysolepis</i> Liebm.	QUCH	40.3	-	-	-
<i>Acer macrophyllum</i> Pursh.	ACMA	43.1	30.2	27.1	5.9
<i>Taxus brevifolia</i> Nutt.	TABR	17.7	28.5	18.1	0.3
<i>Calocedrus decurrens</i> (Torr.) Florin.	CADE	15.6	5.9	6.9	0.7
<i>Abies grandis</i> (Dougl.) Forbes	ABGR	12.2	36.8	1.7	-
<i>Quercus kelloggii</i> Newberry	QUKE	10.4	*	-	-
<i>Alnus rhombifolia</i> Nutt.	ALRH	8.3	*	-	-
<i>Arbutus menziesii</i> Pursh.	ARME	8.3	0.3	-	-
<i>Quercus garryana</i> Dougl.	QUGA	8.3	0.3	-	-
<i>Castanopsis chrysophylla</i> (Dougl.) DC.	CACH	8.3	10.1	6.6	0.7
<i>Cornus nuttallii</i> Aud.	CONU	6.9	7.6	7.6	-
<i>Fraxinus latifolia</i> Benth.	FRLA	6.3	0.7	0.7	-
<i>Pinus lambertiana</i> Dougl.	PILA	3.5	0.3	0.3	-
<i>Chamaecyparis lawsoniana</i> (A. Murr.) Parl.	CHLA	3.1	-	-	-
<i>Pinus ponderosa</i> Dougl.	PIPO	3.1	-	-	-
<i>Salix lucida</i> ssp. <i>lasiandra</i> (Benth.) E. Murr.	SALU	0.3	-	-	-
<i>Betula occidentalis</i> Hook.	BEOC	*	-	-	-
<i>Populus trichocarpa</i> T. & G.	POTR	*	-	3.5	-
<i>Acer glabrum</i> Torr.	ACGL	-	2.1	*	-
<i>Ilex aquifolium</i> L.	ILAQ	-	-	0.3	-
<i>Pinus jeffreyi</i> Grev. & Balf.	PIJE	-	0.7	-	-
<i>Pyrus fusca</i> Raf.	MAFU	-	-	-	0.3
<i>Salix</i> spp. L.	SALIX1	-	-	-	0.3
<i>Picea sitchensis</i> (Bong) Carr.	PISI	-	-	-	3.1
<i>Thuja plicata</i> Donn	THPL	-	10.1	27.1	4.5
<i>Tsuga heterophylla</i> (Raf.) Sarg.	TSHE	-	42.0	57.3	8.3
<i>Alnus rubra</i> Bong	ALRU	4.9	24.3	22.9	28.8
TREE SPECIES		20	18	14	12

Table 2.3 (cont.) b.) Shrub and fern species

SPECIES NAME	SPECIES CODE	STUDY WATERSHED			
		Applegate	South Umpqua	McKenzie	Alsea
<i>Symphoricarpos albus</i> (L.) Blake	SYAL	60.4	11.5	-	2.8
<i>Rubus ursinus</i> Cham. & Schlecht.	RUUR	60.1	77.8	60.4	19.8
<i>Lonicera hispidula</i> (Lindl.) Dougl.	LOHI	39.9	6.3	-	-
<i>Toxicodendron diversilobum</i> (Torr. & Gray) Fosberg	TODI	38.5	10.1	*	-
<i>Rosa gymnocarpa</i> Nutt.	ROGY	40.3	21.5	12.8	1.7
<i>Corylus cornuta</i> var. <i>californica</i> Marsh	COCO	45.1	28.5	29.2	7.6
<i>Berberis nervosa</i> Pursh	BENE	45.1	49.7	53.8	8.3
<i>Berberis aquifolium</i> Pursh	BEAQ	29.2	5.9	-	-
<i>Philadelphus lewisii</i> Pursh	PHLE	29.2	1.0	5.6	*
<i>Holodiscus discolor</i> (Pursh.) Maxim.	HODI	22.9	5.6	2.1	0.3
<i>Whipplea modesta</i> Torr.	WHMO	20.1	18.8	6.9	-
<i>Amelanchier alnifolia</i> Nutt.	AMAL	18.4	3.1	3.1	*
<i>Pachistima myrsinites</i> (Pursh) Raf.	PAMY	16.0	3.8	6.6	-
<i>Linnea borealis</i> L.	LIBO	13.9	45.1	29.5	0.3
<i>Lonicera ciliosa</i> (Pursh) DC.	LOCI	12.2	5.9	4.5	-
<i>Chimaphila umbellata</i> (L.) Bart.	CHUM	7.6	11.5	5.2	-
<i>Polystichum lonchitis</i> (L.) Roth	POLO	6.9	-	-	-
<i>Rosa eglanteria</i> L.	ROEG	5.9	-	-	-
<i>Satureja douglasii</i> (Benth.) Briq.	SADO	5.6	2.1	1.4	-
<i>Rubus parviflorus</i> Nutt.	RUPA	15.6	12.5	10.8	10.8
<i>Symphoricarpos mollis</i> Nutt.	SYMO	4.2	1.0	3.1	-
<i>Polystichum imbricans</i> (D. Eaton)	POIM	3.8	-	-	-
<i>Cornus sericea</i> ssp. <i>occidentalis</i> (Torr. & Gray) Fosberg	COSE	3.8	3.1	*	-
<i>Apocynum androsaemifolium</i> L.	APAN	3.1	0.3	-	-
<i>Garrya fremontii</i> Torr.	GAFR	2.8	0.3	-	-
<i>Ribes roezlii</i> Regel	RIRO	2.8	1.0	-	-
<i>Crataegus douglasii</i> Lindl.	CRDO	2.4	-	-	-
<i>Physocarpus capitatus</i> (Pursh) Kuntze	PHCA	3.8	6.6	1.4	-
<i>Ceanothus sanguineus</i> Pursh	CESA	1.7	-	-	-
<i>Rubus leucodermis</i> Dougl.	RULE	1.4	0.7	1.7	-
<i>Ceanothus integerrimus</i> H. & A.	CEIN	1.0	-	-	-
<i>Salix scouleriana</i> Barratt	SASC	1.0	0.1	*	*
<i>Prunus virginiana</i> var. <i>demissa</i> (Nutt.) Torr.	PRVI	0.7	0.1	-	-
<i>Ribes sanguinum</i> Pursh	RISA	0.7	1.0	*	-
<i>Chimaphila menziesii</i> (R. Br.) Spreng	CHME	0.3	1.7	2.4	-

Table 2.3b (cont.)

SPECIES NAME	SPECIES CODE	STUDY WATERSHED			
		Applegate	South Umpqua	McKenzie	Alsea
<i>Prunus subcordata</i> Benth.	PRSU	0.3	-	-	-
<i>Arctostaphylos glandulosa</i> Eastw.	ARGL	*	-	-	-
<i>Cercocarpus betuloides</i> Nutt.	CEBE	*	-	-	-
<i>Quercus sadleriana</i> R. Br. Campst.	QUSA	*	-	-	-
<i>Rhododendron occidentale</i> (T. & G.) Gray	RHOC	*	-	-	-
<i>Ribes cereum</i> Dougl.	RICE	*	*	-	-
<i>Sambucus cerulea</i> spp. L.	SACE	*	-	-	-
<i>Cornus canadensis</i> L.	COCA	-	-	0.3	-
<i>Rhododendron macrophyllum</i> G. Don	RHMA	-	1.7	2.1	-
<i>Rubus nivalis</i> Dougl.	RUNI	-	2.4	0.7	-
<i>Vaccinium ovalifolium</i> Smith	VA OVA	-	-	*	-
<i>Vaccinium membranaceum</i> Dougl.	VAME	-	1.7	2.4	-
<i>Oplopanax horridum</i> (Smith) Miq.	OPHO	-	-	3.5	*
<i>Prunus emarginata</i> (Dougl.) Walp.	PREM	-	-	-	*
<i>Vaccinium ovatum</i> Pursh	VAOV	-	-	-	*
<i>Ribes lacustre</i> (Pers.) Poir.	RILA	-	2.1	*	0.3
<i>Salix sitchensis</i> Swanson	SASI	0.3	3.1	4.2	1.4
<i>Ribes laxiflorum</i> Pursh	RILAX	-	-	-	1.4
<i>Rubus discolor</i> Weihe & Nees	RUDI	1.4	0.3	-	3.8
<i>Rubus laciniatus</i> Willd.	RULA	0.3	-	-	4.2
<i>Dryopteris austriaca</i> (Jacq.) Woyнар	DRAU	-	0.3	13.5	3.8
<i>Pteridium aquilinum</i> (L.) Kuhn.	PTAQ	2.4	6.6	6.6	6.9
<i>Rhamnus purshiana</i> DC.	RHPU	9.4	6.9	22.6	15.3
<i>Acer circinatum</i> Pursh	ACCI	18.8	64.6	44.8	25.0
<i>Gaultheria shallon</i> Pursh	GASH	6.6	26.7	27.8	13.2
<i>Menziesii ferruginea</i> Smith	MEFE	-	-	-	6.6
<i>Oemleria cerasiformis</i> (H. & A.) Landon	OECE	0.7	13.9	10.1	8.0
<i>Sambucus racemosa</i> L.	SARA	-	*	*	25.3
<i>Ribes bracteosum</i> Dougl.	RIBR	-	2.1	9.7	30.9
<i>Vaccinium parvifolium</i> Smith	VAPA	-	21.9	47.9	33.7
<i>Polystichum munitum</i> (Kaulf.) Presl	POMU	46.2	82.3	72.6	91.0
<i>Athyrium filix-femina</i> (L.) Roth.	ATFI	-	3.1	25.0	62.2
<i>Rubus spectabilis</i> Pursh	RUSP	-	*	16.7	79.9
SHRUB AND FERN SPECIES		51	46	42	34
TOTAL SPECIES		71	64	56	46

Indirect Gradient Analyses

Hectare Scale Ordination

Nonmetric multidimensional scaling produced a two-axis ordination for the hectare scale dataset that explained 94.3% of the variance in the species data based on the Sorenson distance measure (Figure 2.4). The first NMS axis (NMS1_{hs}) (82.2% of total variation explained (TVE)) clearly separated species along the climate gradient from the Applegate to the Alsea watersheds (Figure 2.4, Table 2.4a). Vapor pressure deficit in the summer (VPDSUM) showed a strong positive correlation ($r = 0.87$) with NMS Axis 1 (Table 2.4a), while *Rubus spectabilis* cover (RUSP) showed a strong negative correlation ($r = -0.70$) with the axis. RUSP was strongly correlated with VPDSUM, and its competitive effect may also influence species distributions in the wetter watersheds where it occurs (Pabst and Spies 1998, Nierenberg and Hibbs 2000). VPDSUM also cleanly separated species occurring in the drier interior watersheds where RUSP was absent. Species with highest scores on NMS1_{hs} were all xerophytic species that were most common in southwest Oregon, including *Quercus garryana* Dougl., *Quercus kelloggii* Newberry, *Ceanothus integerrimus* H.&A., *Quercus chrysolepis* Leibm., *Pinus ponderosa* Dougl., and *Apocynum androsaemifolium* L. Species with lowest scores were mesophytic species that were either restricted to or most abundant in cool, humid coastal sites, including *P. sitchensis*, *Sambucus racemosa* L., *R. spectabilis*, *Dryopteris austriaca* (Jacq.) Woyнар, and *Ribes bracteosum* Dougl. NMS2_{hs} (12.1 % TVE) was most strongly correlated with growing degree days (GDDTOT, $r = -0.51$) and fluvial scouring (SCOUR, $r = 0.40$ Table 2.4a). Species with lowest scores on the NMS2_{hs} included *Q. garryana*, *Q. kelloggii*, *C. integerrimus*, *Fraxinus latifolia* Benth., and the exotic species *Rubus discolor* Weihe & Nees. Several of these species occurred in both the relatively warm environments of the Alsea or Applegate watersheds. Species with highest scores on NMS2_{hs} were all species centered in the Cascades watersheds, including *Vaccinium membranaceum* Dougl., *Rhododendron macrophyllum* G. Don, *Acer glabrum* Torr., and *Rubus nivalis* Dougl.

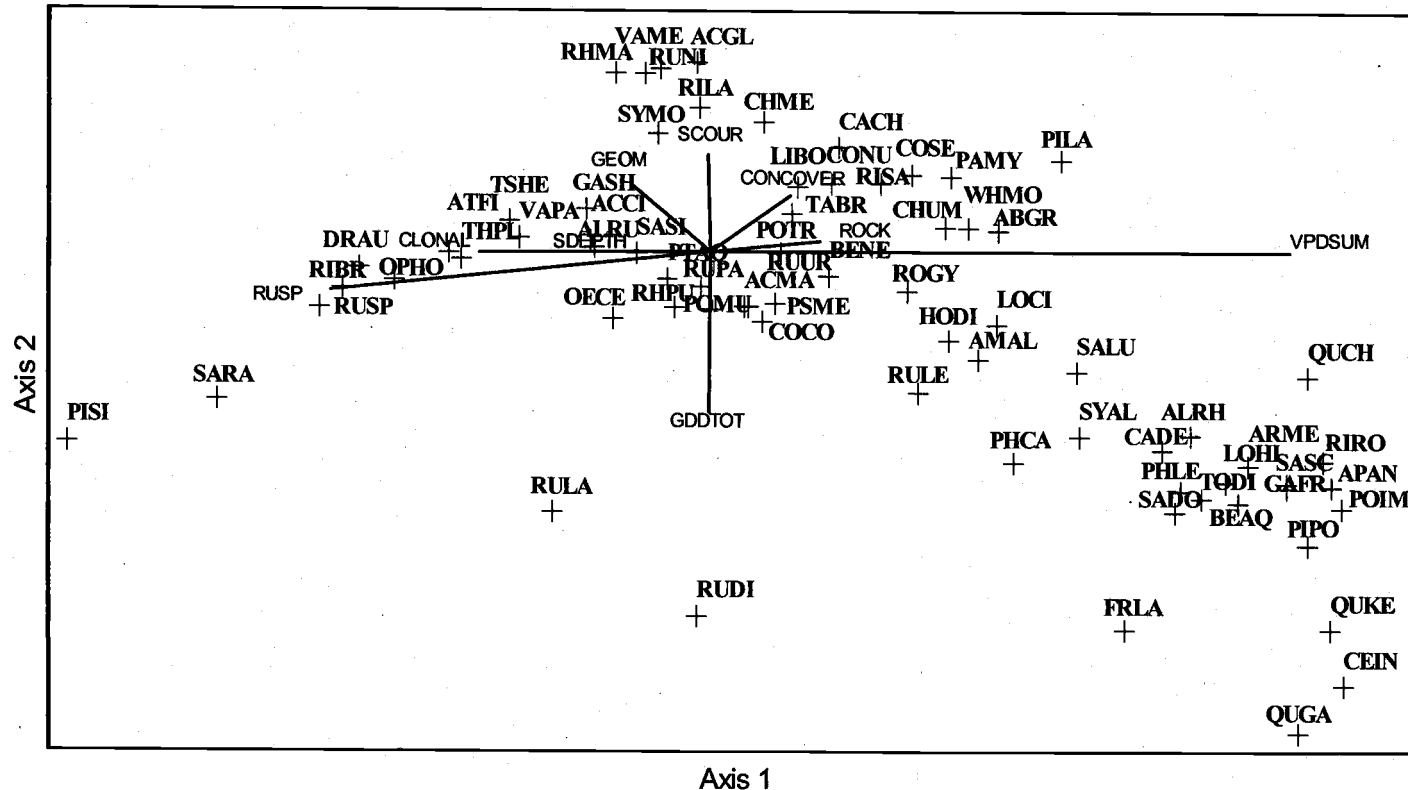


Figure 2.4. Ordination biplot of species distributional centroids based on nonmetric multidimensional scaling (NMS) axes 1 and 2 for hectare samples (n=64) in the four study watersheds. Environmental variables with Pearson's correlation coefficients > 0.32 with either axis are overlaid as vectors. Vector x and y coordinates are proportional to correlation with axes 1 and 2, respectively. Variable code definitions are provided in Table 2.2 and species names are provided in Table 2.3.

Table 2.4a,b. Variance explained by the three NMS Axes and Pearsons correlations coefficients between each axis and the environmental variables: (a) hectare scale ordination. (b) sampling plot scale scale ordination. Variable code definitions provided in Table 2.2.

a.) Hectare Scale Ordination

NMS AXIS	1		2		3	
	r	r ²	r	r ²	r	r ²
Variance explained (%)		82.2		12.1		N/A
CLONAL	-0.54	0.29	-0.10	0.01	-	-
CONCOVER	0.32	0.10	0.25	0.06	-	-
GDDTOT	-0.04	0.00	-0.51	0.26	-	-
GEOM	-0.31	0.10	0.32	0.10	-	-
LDEPTH	0.25	0.06	0.21	0.04	-	-
LOGWA	0.06	0.00	0.11	0.01	-	-
OCOV	0.14	0.02	0.04	0.00	-	-
ROCK	0.38	0.14	0.14	0.02	-	-
RUSP	-0.70	0.50	-0.26	0.07	-	-
SCOUR	-0.04	0.00	0.40	0.16	-	-
SDEPTH	-0.35	0.13	-0.01	0.00	-	-
STRMORD	0.14	0.02	-0.25	0.06	-	-
TCOV	-0.26	0.07	0.00	0.00	-	-
TOPOGRAPHY	0.08	0.01	0.00	0.00	-	-
VPDSUM	0.87	0.76	0.01	0.00	-	-

b.) Sampling Plot Scale Ordination

NMS AXIS	1		2		3	
	r	r ²	r	r ²	r	r ²
Variance explained (%)		35.9		22.1		19.6
BROWSE	-0.49	0.24	-0.19	0.04	-0.15	0.02
CONCOVER	0.34	0.12	0.25	0.06	0.42	0.17
GAP	0.03	0.00	-0.08	0.01	-0.14	0.02
GDDTOT	-0.27	0.07	-0.46	0.21	-0.04	0.00
GEOM	-0.11	0.01	0.14	0.02	-0.03	0.00
HAS	0.24	0.06	-0.10	0.01	0.20	0.04
LDEPTH	0.21	0.04	0.07	0.01	0.19	0.03
LOGWA	-0.08	0.01	-0.03	0.00	0.10	0.01
OCOV	0.08	0.01	0.09	0.01	0.21	0.04
ROCK	0.03	0.00	-0.06	0.00	-0.10	0.01
RUSP	-0.60	0.36	-0.17	0.03	-0.04	0.00
SCOUR	-0.26	0.07	0.13	0.02	-0.37	0.13
SDEPTH	-0.02	0.00	0.03	0.00	-0.02	0.00
STRMORD	-0.11	0.01	-0.25	0.06	0.02	0.00
TCOV	-0.08	0.01	0.10	0.01	0.28	0.08
VPDSUM	0.77	0.59	0.04	0.00	0.01	0.00

Sampling Plot Scale Ordination

Nonmetric multidimensional scaling produced a three axis ordination for the sampling plot scale dataset that explained 76.4% of the variance in the species data based on a Sorenson distance measure (Figure 2.5b, Table 2.4b.). As with the hectare scale ordination, NMS axis 1 (NMS1_{sps}) (35.9% TVE) was most strongly correlated with VPDSUM ($r = 0.77$) and RUSP ($r = -0.60$). Browsing (BROWSE) was also negatively correlated with NMS1_{sps} ($r = -0.49$), but we noted that the herbivory was primarily limited to ungulate browsing on branch tips of *R. spectabilis*, which was nonetheless highly dominant at many coastal sites. Species centroids on NMS1_{sps} were very similar to the hectare-scale ordination, except *Menziesia ferruginea* Smith and *Athyrium filix-femina* (L.) Roth. had very low scores. *A. menziesii* and *Chamaecyparis lawsoniana* (A. Murr.) Parl had very high scores. NMS2_{sps} (22.1% TVE) was moderately correlated with growing degree days (GDDTOT, $r = -0.46$) and appeared to represent a temperature gradient. No other variables showed a correlation coefficient > 0.25 with NMS2_{sps}, but stream order (STRMORD, $r = -0.25$) and conifer cover (CONCOVER) ($r = 0.25$) were weakly correlated with the axis. Species with lowest scores included *Q. garryana*, *T. diversilobum*, *Polystichum imbricans* (D. Eaton), *Q. kelloggii*, and the exotic species *Rosa eglanteria* L. Species with highest scores included *Populus trichocarpa* T. & G., *Oplopanax horridum* (Smith) Miq., *Vaccinium membranaceum* Dougl., *R. nivalis*, and *Tsuga heterophylla* (Raf.) Sarg. NMS3_{sps} (19.6% TVE) appeared to represent a transriparian compositional gradient. Conifer cover showed a positive correlation with the axis ($r = 0.42$) followed by fluvial scouring with a negative correlation ($r = -0.37$). Species with lowest scores on NMS3_{is} included several hardwood trees or shrubs commonly seen on open, cobbly stream margins, including *P. trichocarpa*, *Salix sitchensis* Swanson, and *Salix scouleriana* Barratt, along with the exotic *R. eglanteria*. Species with high scores were all associated with conifer forest habitats, including *V. membranaceum*, *Beberis nervosa* Pursh., *R. nivalis*, and *Gaultheria shallon* Pursh.

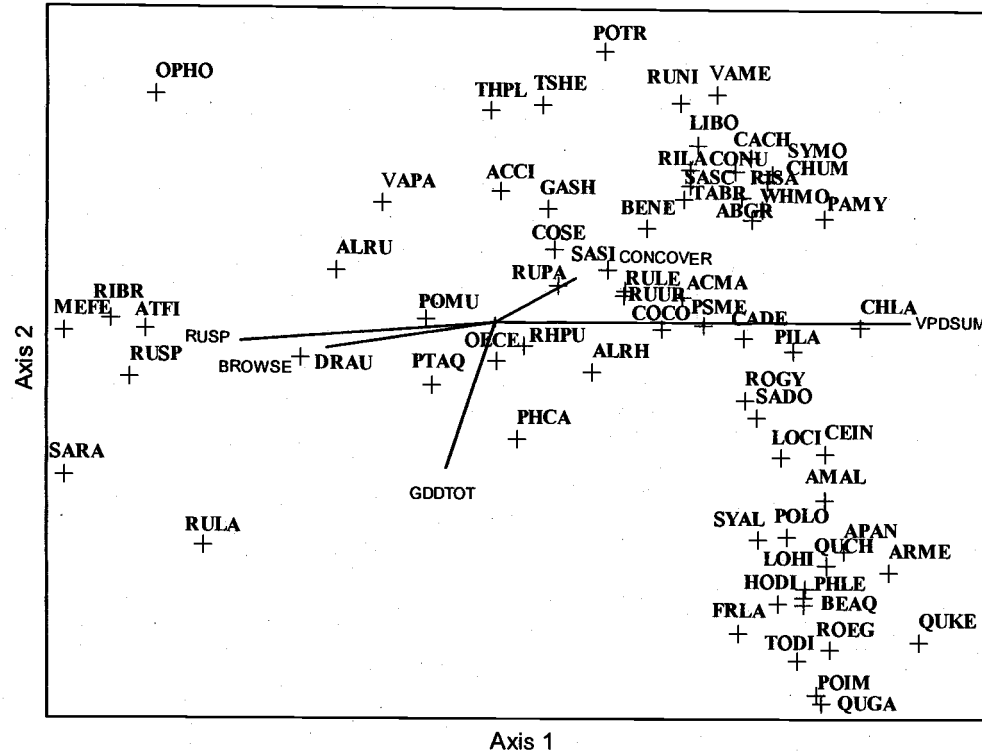


Figure 2.5a. Ordination biplot of species distributional centroids based on nonmetric multidimensional scaling (NMS) axes 1 and 2 for gap and forest samples ($n=480$) in the four study watersheds. Environmental variables with Pearson's correlation coefficients > 0.32 with either axis are overlaid as vectors. Vector x and y coordinates are proportional to correlation with axes 1 and 2, respectively. Variable codes definitions are provided in Table 2.2 and species names are provided in Table 2.3.

Species Associations with Climate, Topography, and Disturbance

Climatic and Topographic Associations of Species

A surprising 94.7% of the species (71 of 75) analyzed showed significant nonhomogeneity in frequency across the climate gradient represented by the four watersheds (Table 2.5a, b.). Only four species, *Rubus parviflorus* Nutt., *R. leucodermis*, *Ribes sanguineum*, and *P. aquilinum* failed to show nonhomogeneity. Three of these four species, however, did show associations with gap disturbance (see below).

Species demonstrated important nonhomogeneity across the topographic gradient as well, with 42.7% of the species (32 out of 75) showing significant associations with either hillslope (23) or streamside (9) environments when values were pooled across watersheds for the three topographic positions in the whole 1152 plot data set (Table 2.4a,b.). Species with strongest affinities to streamside environments included *Alnus rhombifolia* Nutt. ($X^2 = 23.75$, $P < 0.001$), *Physocarpus capitatus* (Pursh) Kuntze ($X^2 = 11.35$, $P = 0.003$), *Cornus sericea* ssp. *occidentalis* (Torr. & Gray) Fosberg ($X^2 = 11.09$, $P = 0.004$), *S. sitchensis* ($X^2 = 16.37$, $P < 0.001$), and *A. rubra* ($X^2 = 89.94$, $P < 0.001$). The majority of the species with significant associations with streamsides were winter deciduous species or ferns.

Many riparian species, especially coniferous and broad-leaved evergreen taxa, showed preferences for hillslope plots. Species with strongest associations with hillslopes included *Pseudotsuga menziesii* (Mirbel) Franco ($X^2 = 14.79$, $P = 0.001$), *R. nivalis* ($X^2 = 8.74$, $P < 0.0013$), *Q. garryana* ($X^2 = 12.10$, $P < 0.002$), and *Satureja douglasii* (Benth.) Briq. ($X^2 = 8.11$, $P = 0.002$) (Table 2.5a,b).

Disturbance Associations of Species

Of the 65 species that occurred at least five times in our gap dataset, 16 (24.6%) showed significant associations with either gap or forest environments (Table 2.5a,b.). Fourteen of the sixteen species occurred with higher frequency in

Table 2.5 a,b. (Cont.)

SPECIES	WATERSHED ASSOCIATION		TOPOGRAPHIC ASSOCIATION		TOPOGRAPHIC PREFERENCE	GAP/FOREST ASSOCIATION			
	X ² (3 d.f.)	P value	X ² (2 d.f.)	P value		Gap	Forest	X ² (1 d.f.)	P - Value
a.) Trees (cont.)									
<i>Quercus garryana</i>	68.81	<0.001	12.10	0.002	Hillslope	5	4	0.000	N.S.
<i>Quercus kelloggii</i>	92.41	<0.001	8.83	0.012	Hillslope	9	4	1.27	N.S.
<i>Taxus brevifolia</i>	86.71	<0.001	7.54	0.023	Hillslope	44	74	9.45	0.002
<i>Thuja plicata</i>	130.01	<0.001	2.74	NS.	N/A	21	17	0.26	N.S.
<i>Tsuga heterophylla</i>	325.13	<0.001	12.88	0.002	Hillslope	66	76	0.81	N.S.
b.) Shrubs and ferns									
<i>Acer circinatum</i>	157.50	<0.001	3.24	N.S.	N/A	103	108	0.14	N.S.
<i>Amelanchier alnifolia</i>	102.71	<0.001	3.27	N.S.	N/A	16	9	1.52	N.S.
<i>Apocynum androsaemifolium</i>	23.00	<0.001	3.83	N.S.	N/A	9	1	5.00	0.025
<i>Athyrium filix-femina</i>	405.45	<0.001	32.23	<0.001	Streamside	73	57	2.37	N.S.
<i>Berberis aquifolium</i>	171.30	<0.001	6.90	0.032	Hillslope	23	20	0.10	N.S.
<i>Berberis nervosa</i>	158.37	<0.001	49.14	<0.001	Hillslope	89	105	1.95	N.S.
<i>Ceanothus integerrimus</i>					N/A	5	0	3.23	0.072
<i>Ceanothus sanguineus</i>	15.07	0.002	2.81	N.S.	N/A				N/A
<i>Chimaphila menziesii</i>	9.86	0.020	4.82	0.090	N/A				N/A
<i>Chimaphila umbellata</i>	34.86	<0.001	17.01	<0.001	Hillslope	29	15	4.23	0.040
<i>Corylus cornuta</i> var. <i>californica</i>	102.22	<0.001	21.29	<0.001	Hillslope	72	52	3.93	0.048
<i>Cornus sericea</i> ssp. <i>occidentalis</i>	21.13	<0.001	11.09	0.004	Streamside	6	4	0.10	N.S.
<i>Crataegus douglasii</i>	21.13	<0.001	0.29	N.S.	N/A				N/A
<i>Dryopteris austriaca</i>	81.47	<0.001	0.37	N.S.	N/A	6	14	2.56	N.S.
<i>Garrya fremontii</i>	20.05	<0.001	2.02	N.S.	N/A				N/A

Table 2.5 a,b. Results of X^2 test of the null hypothesis of homogeneity in species frequency across climatic settings (the four study watersheds) and topographic positions (streamside, midslope, and hillslope sampling plots) in the riparian inventory, and gap vs. forest settings for the gap inventory. Frequencies presented for gap and forest settings are number of plots with species out of 240 gap or forest sampling plots. Tests are for all species that occurred at least 5 times in the respective dataset (n= 75 species for the riparian inventory and n = 65 for the gap/forest dataset). Topographic preference is provided for significant topographic associations. a.) Trees, b.) Shrubs and ferns

SPECIES	WATERSHED ASSOCIATION		TOPOGRAPHIC ASSOCIATION		TOPOGRAPHIC PREFERENCE	GAP/FOREST ASSOCIATION			
	X ² (3 d.f.)	P value	X ² (2 d.f.)	P value		Gap	Forest	X ² (1 d.f.)	P - Value
a.) Trees									
<i>Abies grandis</i>	224.54	<0.001	10.23	0.006	Hillslope	49	33	3.31	0.069
<i>Acer glabrum</i>	18.09	<0.001	1.01	N.S.	N/A				N/A
<i>Acer macrophyllum</i>	105.18	<0.001	8.36	0.015	Streamside	99	69	7.70	0.009
<i>Alnus rhombifolia</i>	73.53	<0.001	23.75	< 0.001	Streamside	7	5	0.09	N.S.
<i>Alnus rubra</i>	59.58	<0.001	89.94	< 0.001	Streamside	47	36	1.46	N.S.
<i>Arbutus menziesii</i>	68.81	<0.001	4.99	0.083	N/A	10	1	5.96	0.015
<i>Castanopsis chrysophylla</i>	23.86	<0.001	9.73	0.008	Hillslope	24	15	1.79	N.S.
<i>Calocedrus decurrens</i>	49.00	<0.001	4.39	N.S.	N/A	18	24	0.65	N.S.
<i>Chamaecyparis lawsoniana</i>	27.21	<0.001	0.67	N.S.	N/A	4	2	0.17	N.S.
<i>Cornus nuttallii</i>	22.76	<0.001	3.61	N.S.	N/A	22	13	1.97	N.S.
<i>Fraxinus latifolia</i>	39.11	<0.001	1.21	N.S.	N/A	12	6	1.44	N.S.
<i>Pinus lambertiana</i>	22.23	<0.001	3.54	N.S.	N/A				N/A
<i>Pinus ponderosa</i>	27.21	<0.001	6.05	0.049	Hillslope				N/A
<i>Picea sitchensis</i>	27.21	<0.001	0.67	N.S.	N/A				N/A
<i>Populus trichocarpa</i>	30.26	<0.001	3.23	N.S.	N/A	4	2	0.17	N.S.
<i>Pseudotsuga menziesii</i>	196.08	<0.001	14.79	0.001	Hillslope	95	96	0.000	N.S.
<i>Quercus chrysolepis</i>	386.97	<0.001	1.52	N.S.	N/A	34	18	4.85	0.028

Table 2.5b. (Cont.)

SPECIES	WATERSHED ASSOCIATION		TOPOGRAPHIC ASSOCIATION		TOPOGRAPHIC PREFERENCE	GAP/FOREST ASSOCIATION			
	X ² (3 d.f.)	P value	X ² (2 d.f.)	P value		Gap	Forest	X ² (1 d.f.)	P - Value
b.) Shrubs and ferns (cont.)									
<i>Gaultheria shallon</i>	61.64	<0.001	6.90	0.032	Hillslope	39	37	0.02	N.S.
<i>Holodiscus discolor</i>	129.99	<0.001	4.41	N.S.	N/A	21	10	3.45	0.063
<i>Linnea borealis</i>	187.67	<0.001	20.86	<0.001	Hillslope	62	52	0.93	N.S.
<i>Lonicera ciliosa</i>	40.88	<0.001	0.13	N.S.	N/A	12	11	0.00	N.S.
<i>Lonicera hispidula</i>	241.69	<0.001	4.50	N.S.	N/A	30	21	1.40	N.S.
<i>Menziesii ferruginea</i>	57.96	<0.001	1.39	N.S.	N/A	1	6	2.32	N.S.
<i>Oemleria cerasiformis</i>	35.45	<0.001	0.97	N.S.	N/A	28	24	0.19	N.S.
<i>Oplopanax horridum</i>	30.26	<0.001	3.23	N.S.	N/A	3	3	0.17	N.S.
<i>Pachistima myrsinites</i>	65.03	<0.001	11.35	0.003	Hillslope	11	10	0.00	N.S.
<i>Physocarpus capitatus</i>	25.34	<0.001	11.35	0.003	Streamside	7	6	0.00	N.S.
<i>Philadelphus lewisii</i>	199.11	<0.001	9.36	0.009	Streamside	25	21	0.22	N.S.
<i>Polystichum imbricans</i>	28.97	<0.001	4.55	N.S.	N/A				N/A
<i>Polystichum lonchitis</i>	61.06	<0.001	1.32	N.S.	N/A	2	6		N/A
<i>Polystichum munitum</i>	164.95	<0.001	2.65	N.S.	N/A	155	189	11.17	<0.001
<i>Pteridium aquilinum</i>	7.48	0.058	9.23	0.010	Hillslope	18	19	0.00	N.S.
<i>Rhododendron macrophyllum</i>	11.29	0.010	9.00	0.011	Hillslope				N/A
<i>Rhamnus purshiana</i>	35.77	<0.001	4.58	N.S.	N/A	41	33	0.78	N.S.
<i>Ribes bracteosum</i>	180.54	<0.001	23.97	<0.001	Streamside	25	19	0.63	N.S.
<i>Ribes lacustre</i>	14.23	0.003	2.01	N.S.	N/A	4	2	0.17	N.S.
<i>Ribes roezlii</i>	20.05	<0.001	0.67	N.S.	N/A				N/A
<i>Ribes sanguinum</i>	5.42	N.S.	0.40	N.S.	N/A	16	1	12.43	<0.001
<i>Rosa eglanteria</i>	51.76	<0.001	0.12	N.S.	N/A	5	11	1.62	N.S.
<i>Rosa gymnocarpa</i>	148.19	<0.001	19.97	<0.001	Hillslope	63	37	7.90	0.005
<i>Rubus discolor</i>	18.76	<0.001	0.89	N.S.	N/A				N/A

Table 2.5b. (Cont.)

SPECIES	WATERSHED ASSOCIATION		TOPOGRAPHIC ASSOCIATION		TOPOGRAPHIC PREFERENCE	GAP/FOREST ASSOCIATION			
	X ² (3 d.f.)	P value	X ² (2 d.f.)	P value		Gap	Forest	X ² (1 d.f.)	P - Value
a.) Shrubs and ferns (cont.)									
<i>Rubus laciniatus</i>	31.98	<0.001	0.16	N.S.	N/A	2	5	0.80	N.S.
<i>Rubus leucodermis</i>	5.42	N.S.	5.14	0.077	N/A	14	1	9.91	0.002
<i>Rubus nivalis</i>	14.67	0.002	8.74	0.013	Hillslope	1	4	0.81	N.S.
<i>Rubus parviflorus</i>	4.18	N.S.	4.33	N.S.	N/A	56	33	6.68	0.001
<i>Rubus spectabilis</i>	676.25	<0.001	2.07	N.S.	N/A	84	60	5.25	0.022
<i>Rubus ursinus</i>	210.52	<0.001	1.52	N.S.	N/A	135	130	0.14	N.S.
<i>Satureja douglasii</i>	21.88	<0.001	8.11	0.017	Hillslope	7	4	0.37	N.S.
<i>Sambucus racemosa</i>	233.82	<0.001	2.22	N.S.	N/A	19	13	0.84	N.S.
<i>Salix scouleriana</i>					N/A	6	0	4.22	0.04
<i>Salix sitchensis</i>	11.49	0.009	16.37	<0.001	Streamside	5	11	1.62	N.S.
<i>Symphoricarpos albus</i>	454.56	<0.001	1.11	N.S.	N/A	47	36	1.46	N.S.
<i>Symphoricarpos mollis</i>	15.32	0.002	1.79	N.S.	N/A	8	1	4.01	0.044
<i>Toxicodendron diversilobum</i>	268.71	<0.001	12.55	0.002	Hillslope	43	27	3.76	0.052
<i>Vaccinium membranaceum</i>	12.80	0.005	3.54	N.S.	N/A	8	6	0.07	N.S.
<i>Vaccinium parvifolium</i>	185.07	<0.001	8.97	0.011	Hillslope	63	68	0.17	N.S.
<i>Whipplea modesta</i>	79.54	<0.001	8.83	0.012	Hillslope	38	13	12.64	<0.001

gaps than in the adjacent forest. *Taxus brevifolia* Nutt. and the fern *Polystichum munitum* (Kaulf.) Presl. were the only species that occurred with significantly greater frequency in forest interiors, and this association was strong in both cases ($X^2 = 9.45$, $P = 0.0021$, and $X^2 = 11.17$, $P < 0.001$, for *T. brevifolia* and *P. munitum*, respectively).

DISCUSSION

Western Oregon comprises a climatic and biogeographic tension zone between the mediterranean and maritime provinces of the Pacific slope (McLaughlin 1989, Franklin and Dyrness 1988). This transitional nature was clearly evident in changes in the vegetation composition of riparian forests across the four watersheds. Our finding that there are three major floristic elements in the western Oregon riparian flora (Figure 2.3) is consistent with Franklin and Dyrness' (1988) treatment of upland vegetation. Our recognition of coastal, Cascades, and Klamath floristic elements, roughly parallel the Sitka spruce, western hemlock, and mixed conifer zones they described. Both treatments suggest that there are two major biogeographic boundaries in low elevation forest vegetation of western Oregon: (1) a north-south running boundary west of the crest of the coastal mountains that marks the landward extent of coastal fogs and associated species (e.g., *Picea sitchensis*), and (2) an east-west boundary located along the Rogue/South Umpqua watershed divide in southwest Oregon that marks the southern extent of many widespread northern taxa (e.g., *Tsuga heterophylla*). However, we noted some minor differences from the patterns described by Franklin and Dyrness (1988). We observed that although much of the Alsea Watershed is in their western hemlock zone, the dominance of *R. spectabilis* in riparian forests of the Alsea watershed make them floristically distinct from the riparian forests of the Cascades. Also, the South Umpqua Watershed, placed in the mixed conifer zone

along with the nearby Applegate Watershed by Franklin and Dyrness (1988), showed greater floristic similarity with the more distant McKenzie Watershed (Figure 2.3).

Our indirect gradient analyses showed that variation in hectare scale vegetation composition was correlated primarily with vapor pressure deficit in summer and with growing degree days but also with *R. spectabilis* cover within the hectare (Table 2.4a). In our sampling plot scale analysis, the topographic gradient also appeared as an important source of vegetation variation, but it explained less variance in species composition than did the geographic gradient represented by vapor pressure deficit in summer (Table 2.4b). Moreover, X^2 analyses confirmed that more species showed the landscape scale habitat preferences (watershed associations) than associations with topographic position (94.7% vs. 42.7% of species tested) or gap vs. forest setting (94.7% vs. 24.6% of species tested) (Table 2.5a-b). Collectively, these results suggest that landscape scale factors (climate) drive the primary compositional differences among sites, with topographic and disturbance gradients causing secondary, but locally important floristic variation within them.

Landscape Scale Controls on Riparian Species Distributions

Our finding that riparian plant distributions were controlled primarily by climate and secondarily by local environmental gradients is in accordance with the relatively few other regional scale analyses of riparian vegetation distributions (Collins et al. 1981, Alcaraz et al. 1997). Collins et al. (1981) noted that eastern deciduous forest species in Oklahoma reached their westernmost extent in riparian forests, but eventually dropped out as climate grew increasingly arid further west. Alcaraz et al. (1997) also noted a rapid change in species composition from mesic high elevation riparian forests to low elevation riparian forests of southeast Spain.

Why should climate be such an important controller of riparian forest plant composition? As in upland forests, climate probably operates through direct physiological and indirect ecological mechanisms. Collins et al. (1981) speculated that rainfall on higher floodplain terraces was necessary to support eastern deciduous species in the riparian forest, and that the decline in precipitation was associated with their absence from bottomland forests in western Oklahoma. Subsequent stable isotope work in the southwest U.S. has demonstrated the importance of atmospheric as well as hydrologic inputs to the water balance of riparian trees (Kolb et al. 1997). In addition to water balance, other physiological influences of climate (e.g., frost) are undoubtedly important. Along the mountain streams sampled in this study, where floods are relatively short-lived, climate may exert the predominant influence on the vegetation throughout the year.

Among the most important indirect ecological effects of climate on vegetation are its influences on interspecific competition. Increases in vegetation density from dry to wet climates have been reported (see Waring et al. 2002), and it is likely that the presence or increased dominance of particularly competitive species in the wettest climates are important mechanisms driving vegetation change across the gradient. We noted a strong increase in dominance of *R. spectabilis* across the gradient coincident with declines in frequency of many southern species (Table 2.3). Although common in both the McKenzie and Alsea watersheds, the *R. spectabilis* was typically smaller and topographically restricted to wet swales and streamsides in the former watershed yet grew vigorously from streamsides to hillslopes in the latter, suggesting the wetter climate of the coastal mountains partially explains the species' strong dominance there (Tappeiner et al. 1991, Pabst and Spies 1998, Nierenberg and Hibbs 2000).

Local Scale Controls on Species Distributions

After accounting for landscape scale variables and *R. spectabilis* cover, the primary local driver of compositional change in this study appeared to be the topographic gradient from streamsid es to hillslopes. This complex gradient is coincident with decreases in fluvial disturbance and soil moisture and increases in conifer cover, overstory cover, total cover, and litter depth. Together these environmental changes appeared to be important for many species, as indicated by significant associations with either streamside or hillslope topographic positions for almost half the species tested.

Gap disturbance appeared to have a little effect on species composition overall, at least in the ordination analyses we performed (Figure 2.5a,b.), but was important for a number of species. *R. leucoder mis* and *R. sanguineum* occurred an order of magnitude more often in gaps than forest settings, indicating these species are closely tied to riparian forest openings (Table 2.5b). Many other species also had higher frequencies in natural forest gaps, but most of these differences were relatively minor. Our observation that *R. spectabilis* was significantly associated with gaps fits with other studies that have reported the species is relatively shade intolerant (Minore and Weatherly 1994, Pabst and Spies 1998, Hibbs and Bower 2001). Where climate is suitably moist for it to grow vigorously, this species' ability to rapidly exploit disturbance gaps and to persist (Tappeiner et al. 1991) may partially explain its strong dominance in riparian forests of Oregon's coastal mountains. *T. brevifolia* and the fern *P. munitum* were the only species with significant associations with forest environments, suggesting they are both intolerant of the more stressful microclimates in open environments and that they are highly shade tolerant, as suggested by published literature (Waring and Major 1964, Minor e 1979). We also noted that *P. munitum* was frequently the only species that occurred under the dense *R. spectabilis* thickets of the coastal riparian forests.

We conclude that the riparian forests of western Oregon show important landscape scale variation in composition with three major floristic elements across the region: (1) a coastal element, (2) a Cascades element, and (3) a Klamath element. Species composition overall showed strong correlations with climatic variables (vapor pressure deficit and growing degree days) and *R. spectabilis* cover at the hectare and sampling plot scales, with additional sampling plot scale variation best explained by fluvial scouring and conifer cover. Most species showed statistically significant associations with climatic setting (study watersheds), many showed significant associations with topographic position, and some showed significant associations with gap or forest setting. This study supports a multiscale perspective of controls on riparian plant species distributions whereby climate drives major vegetation change among riparian forests and topographic and disturbance gradients govern local distributions within them. This perspective adds a geographic dimension to a developing conceptual foundation of riparian ecology in the Pacific Northwest (Gregory et al. 1991, Fetherston et al 1995, Pabst and Spies 1998, 1999, Dykaar and Wigington 2000, Johnson et al. 2000, Naiman et al. 2000, Nierenberg and Hibbs 2000, Hibbs and Bower 2001).

CHAPTER THREE - MULTISCALE CONTROLS ON WOODY PLANT DIVERSITY IN WESTERN OREGON RIPARIAN FORESTS

INTRODUCTION

Riparian forests are believed to be among the most floristically diverse terrestrial ecosystems (Gregory et al. 1991, Naiman et al. 1993, Mouw and Alaback 2002), but ecologists are only beginning to unravel the sources of this complexity. Riparian vegetation is shaped by factors acting at multiple scales, from local fluvial, geophysical, and gap disturbances to landscape gradients in climate and geology (Baker 1989, Bendix 1994, Fetherston et al. 1995, Pabst and Spies 1998, Dykaar and Wigington 2000, Johnson et al. 2000, Wimberly and Spies 2001, Dixon et al. 2002). An integrated understanding of these multiscale factors is lacking, yet fundamental to conserving riparian plant diversity.

In upland environments, a growing body of theoretical and empirical work has explored how local and landscape or regional scale factors influence species diversity at different scales (Ricklefs 1987, Caley and Schluter 1997, Cornell 1999, Huston 1999a, Sarr et al. in press). Most field studies and associated biodiversity theory have focused on the effects of local controls such as soil resource or light availability, competition, and disturbance dynamics on floristic diversity (Grime 1973, Huston 1979, 1999a, Tilman 1982, 1987, Stevens and Carson 2002). Larger scale studies have illustrated how historical or climatic factors may also act to constrain diversity (Ricklefs 1987, Kleidon and Mooney 2000). All these factors probably influence riparian ecosystems, yet few studies have explored plant diversity in riparian settings (see Pollock et al. 1998, Mouw and Alaback 2002).

Most analyses of riparian vegetation highlight local fluvial processes, environmental gradients, and the heterogeneity they jointly create (Gregory et al. 1991, Fetherston et al. 1995, Patten 1998, Johnson et al. 2000). Riparian disturbance processes are believed to limit competitive exclusion in the riparian

zone, and they have been linked to non-equilibrium models of species diversity (e.g., Connell 1978, Huston 1979) in several geographic settings (Nilsson et al. 1989, Pollock et al. 1998).

Local factors maintaining environmental heterogeneity also appear important for floristic diversity in upland (Huston 1994, Tilman 1994) and riparian plant communities (Gould and Walker 1997). In riparian forests, heterogeneity is expressed at the smallest scales by variation in geomorphology, substrates, or light at individual sites, and by the dynamic mosaic of disturbance, light, soil moisture, or soil drainage conditions on floodplains (Hack and Goodlet 1960, Hawk and Zobel 1974, Fonda 1974, Duncan 1993, Harris 1987, Sakai et al. 1999). In addition, the change in light availability, substrate characteristics, and moisture availability from streambanks to hillslopes may influence the rate of species turnover (beta diversity *sensu* Whittaker 1960, Wilson and Shmida 1984) across the riparian zone.

A more complete, multiscale understanding of the factors controlling riparian plant diversity would link local patterns and mechanisms with landscape scale controls (see Bendix 1994). It is unclear, for example, how strongly landscape scale controls on plant distribution, such as climate, interact with or regulate local structures and processes. Are landscape scale controls primary or secondary influences? Do they influence species directly by physiological mechanisms? Or do they act indirectly, by controlling local conditions (e.g., competitive dynamics and gradient structure) in the riparian ecosystem?

STUDY OBJECTIVES AND HYPOTHESES

Our goal in this study was to explore the relationships of species diversity with local and landscape scale environmental variables in riparian forests of western Oregon. Because many of these multiscale factors are not completely independent, we employed the method of multiple working hypotheses to evaluate

the most important factors driving riparian plant diversity, and their interactions. In four watersheds spanning a steep climate gradient, we sampled woody plant diversity at two scales, (1) local environments (40 m² sampling plots) and (2) hectare scale stream reaches, to gain a better understanding of processes affecting riparian subhabitats (streamsides, midslopes, and hillslopes) and the riparian forest as a whole. We analyze and report species richness as our index of diversity and use the two terms interchangeably throughout this paper.

Hypothesis 1: Riparian plant diversity is structured primarily by local conditions.

A local model of species diversity suggests that conditions within the riparian forest are primary determinants of floristic diversity. Examples of local controls on diversity include effects of flooding, volume of large woody debris, geomorphic heterogeneity, and canopy gaps (Nilsson et al. 1989, Gregory et al. 1991, Pollock et al. 1998, Mouw and Alaback 2002). If local controls are most important, then the influences of these phenomena will explain more variation in local and stream reach scale richness than geographic variation associated with climate.

Hypothesis 2: Riparian plant diversity is structured primarily by regional climate through direct controls.

Most direct control climate models predict that vascular plant species richness is highest in climates where moisture and temperature are least limiting (Gentry 1988, O'Brien 1998). Collins et al. (1981) noted a decline in the richness of riparian forests from east to west across a steep climate gradient in Oklahoma and speculated that aridity limits the distribution of a number of eastern riparian tree species. An increase in diversity from the dry climates of southwest Oregon to the wetter, more productive climates of northwest Oregon would be predicted by

general climate-driven models of plant species richness (O'Brien 1998). If direct climatic control is most important, then the geographic climate gradient will explain more variation in richness than local factors within riparian forests.

Hypothesis 3: Riparian plant diversity is structured primarily by regional climate through indirect controls on local conditions.

Climate can indirectly control riparian plant diversity through influences on the local riparian environment. In upland environments of the Pacific Northwest, climate is believed to govern directly spatial patterns of species composition, growth rate, leaf area, and understory resources (Grier and Running 1977, Franklin and Dyrness 1988, Waring et al. 2002), all of which may potentially control diversity. Climate also potentially affects riparian plant diversity through its influence on topographic moisture gradients. Moisture heterogeneity and plant species differentiation (beta diversity) across topographic gradients are known to decline from dry to wet climate regions of the Pacific Northwest (Whittaker 1960, del Moral and Fleming 1979, Ohmann and Spies 1998). We know of no regional studies comparing topographic moisture gradients in riparian forests, but it is likely that the gradient from wet streamsides to drier hillslopes decreases in magnitude as one moves from dry to wet climates, with an associated decline in beta diversity.

There would be a unimodal or negative pattern in diversity across the climate gradient from drier to wetter, more productive climates if climate's influences on competitive dynamics and on moisture heterogeneity are important indirect controls on diversity.

If competitive pressures are the primary limitations on diversity in wet, productive climates, nonequilibrium models (e.g., Huston 1979) predict that disturbance should play a stronger role in maintaining diversity in these settings than in less productive locales. Consequently, the increase in local diversity with disturbance should be greatest in such areas.

We pose three subhypotheses about the environmental changes in riparian forests that indirectly control diversity moving from dry to wet climates of western Oregon. Subhypothesis 3a: forests will become denser, with less understory light and lower alpha diversity, Subhypothesis 3b: topographic moisture gradients will become muted with a concomitant decline in beta diversity from streamsides to hillslopes, Subhypothesis 3c: differences in richness between disturbance gaps and forest interiors will increase.

METHODS

Field Sampling

In the summers of 1999 and 2000, we sampled riparian vegetation in four major watersheds of western Oregon: (1) the Applegate in the eastern Siskiyou Mountains, (2) the South Umpqua in the southern Cascades; (3) the McKenzie in the central western Cascades, and (4) the Alsea in the western Coast Range (Figure 3.1). The watersheds range in size from ca. 180,000 ha (Alsea) to 470,000 ha (South Umpqua). Sampling was conducted in low to moderate elevation areas of roughly similar mean annual temperature (9-10.5 ° C), but precipitation and seasonal temperature regimes were distinct in each study watershed. Annual precipitation and precipitation days increase from south to north, while summer temperatures and vapor pressure deficits decline. Within these four watersheds, we sampled woody riparian vegetation in three related field studies: (a) a broad riparian inventory, (b) a gap study which used paired comparisons of forest gaps and forest interiors, and (c) light and moisture gradient quantification studies.

Riparian Inventory

In 1999, we sampled vegetation and environmental characteristics at sixteen 1st through 5th order stream reaches in each of the four study watersheds. Stream order and watershed area were determined for each stream at the sample reach from USGS 1:24,000 topographic quadrangle maps. For each watershed, we interviewed staff at the appropriate land management agency (USDA Forest Service or USDI Bureau of Land Management) to determine management histories of each potential sample

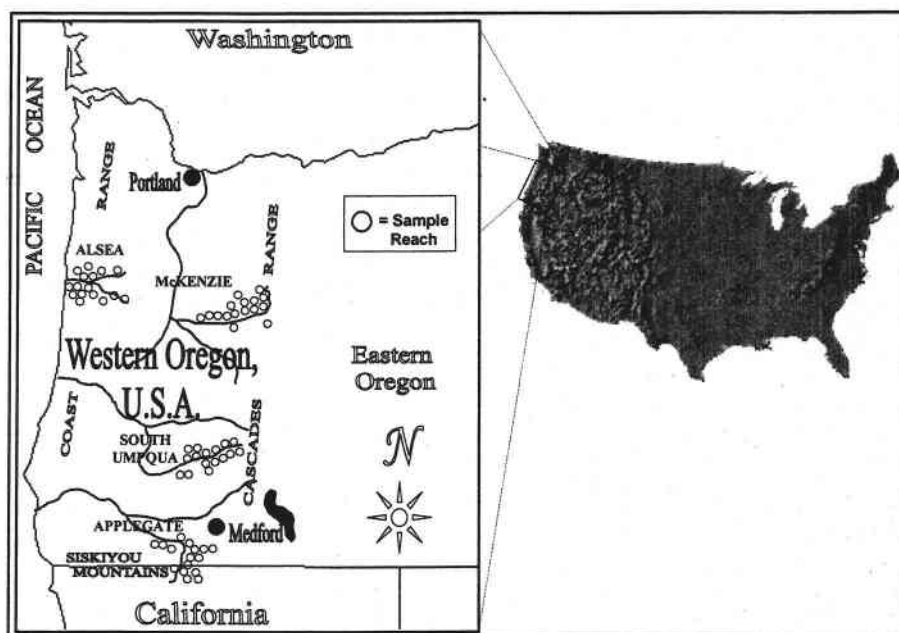


Figure 3.1. Study area and location of study watersheds and sample reaches. Dark circles denote major regional cities.

reach. We then confined field sampling to stream reaches that had not had timber harvest or other management within the last 30 years and which occurred within 1 hour hiking distance (3-4 km) of an access road or trail (Figure 3.2). In each watershed, this yielded 30-50 potential sample reaches. Sample reaches were assigned numbers and sixteen numbers were selected at random for field study sites

in each watershed (64 total). All plots were placed at least 50 meters upstream or downstream from a road or trail crossing and then a random distance from zero to 200 m further upstream or downstream (Figure 3.2). Although the distribution of stream orders differed substantially between the study watersheds, most streams selected in each (56 % – 94%) were second or third order streams.

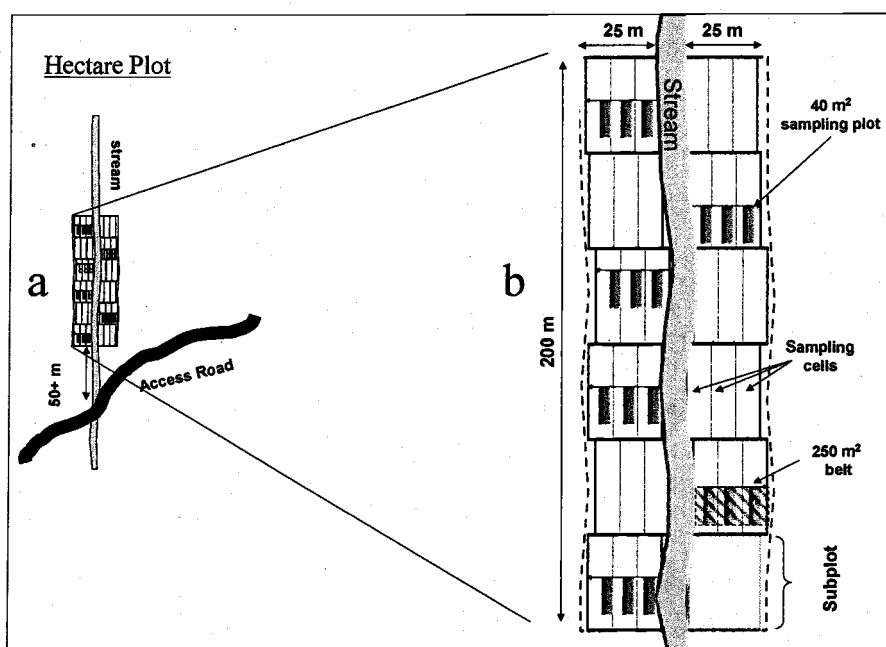


Figure 3.2. Diagram illustrating the location of: (a) the hectare plot relative to an access road and sample stream, and (b) the arrangement of the subplots, sampling cells, and 40 m² sampling plots within the hectare plot.

At each sample reach, we established a plot that straddled the stream and was 200 m long by 50 m wide, not including the stream channel, thereby encompassing a hectare of riparian forest habitat. All distances were slope distances measured along the ground surface with a fiberglass tape. Hereafter we will refer to this plot as the hectare plot. Slope-corrected areas for the plots in each watershed averaged just over 90% of uncorrected areas and were not significantly different among watersheds (mean \pm s.d. = 9188 ± 452 m², 9066 ± 640 m², $9164 \pm$

753 m², and 9001± 653 m² for the Alsea, McKenzie, South Umpqua, and Applegate watersheds, respectively).

We established six pairs of 25 x 33.3 m subplots (thus 12 in the whole hectare plot) with the 33.3 m side parallel to the stream (Figure 3.2). We randomly selected one subplot of each pair for sampling of vegetation and environmental characteristics. We divided the subplot to produce three contiguous 8 x 33.3 m sampling cells at increasing distances from the stream edge and then randomly placed three sampling plots (4 x 10 m = 40 m²) in each subplot with one sampling plot per sampling cell. Presence and cover of all woody species and additional environmental data were collected in sampling plots arrayed with the long side parallel to the stream. There were a total of 64 one hectare plots and 1152 sampling plots.

Along these mountain streams, the three sampling plots usually corresponded with a horizontal and vertical gradient from (1) streamside bars to (2) midslopes/flood plain terraces and (3) lower hillslopes. Although the placement of plots varied somewhat with the morphology of the valley floor along a particular stream, we will refer to the three topographic positions as (1) streamside, (2) midslope, and (3) hillslope plots.

We determined the number of geomorphic units occurring in each sampling plot using a key to geomorphic units we developed in the field (e.g., channel shelf, streamside terrace, toeslope, hillslope). There were typically 1-3 geomorphic units per sampling plot. Ground distance from the plot center to the current water's edge was recorded, and slope in degrees from the plot center to the stream edge was estimated using a clinometer held at 1 meter above the ground. Overstory cover was an ocular estimate of tree cover straight up from a point 1.75 m above the ground viewed through a 20 cm diameter ring held vertically at arms length (ca. 45 cm). Total cover was estimated by applying the same method with the observer seated and included any shrub layers greater than 1.2 m above the ground, in addition to overstory cover.

Soil characteristics were determined by digging a 30 cm soil pit in the middle of each sampling plot. From this pit, soil texture was estimated by hand. Litter depth and, where a bedrock layer was encountered, depth to bedrock, were measured. Where a bedrock layer was not encountered, an estimate of 35 cm was recorded.

We also recorded two indices of disturbance in each sampling plot. An index of fluvial scouring was developed by noting the proportion of each sampling plot that was visibly affected by fluvial activity, including obvious signs of fluvial erosion or deposition or flow channels. In a similar way, we recorded presence of herbivory by noting percent of sampling plot with browsing of shrubs and trees. In both cases, the index scores were: (1) disturbance noted in 0-20 percent of sampling plot, (2) 20-40 percent, (3) 40-60 percent, (4) 60-80 percent, and (5) 80-100 percent.

After we sampled the three sampling plots in a subplot, two observers performed a two minute "sweep" of a 25 m x 10 m belt from the upper subplot edge back to the stream looking for additional species. From the 18 sampling plots and six sweeps we developed a preliminary species list for the hectare plot. Then two samplers simultaneously performed a 20-25 minute time-constrained search for additional species (presence/absence) in the entire hectare plot. In most cases, the time-constrained search of the hectare plot added two to three additional species to the preliminary list generated from the sampling plots. We adjusted the search time up to 5 minutes for ruggedness of the terrain and abundance of downed wood, with especially difficult plots receiving the longer search time. We believe that the additional 5 minutes used in difficult plots did not bias estimates of species richness, for the most rugged plots usually required at least 5 additional minutes to safely traverse. Table 3.1 summarizes the numbers of sampling units at each scale for the two field inventories.

Table 3.1 Summary of sample units for the two field inventories. Hectare plot, subplot, and sample plot locations in the riparian inventory are illustrated in Figure 3.2.

FIELD INVENTORY		
	<u>Riparian Inventory</u>	<u>Gap Study</u>
	4 watersheds	4 watersheds
	16 sample reaches/watershed	6 stream reaches per watershed
	1 hectare plot/sample reach	10 gap samples/stream reach
	6 subplots sampled per hectare plot	
	3 sampling plots/subplot sampled	
TOTAL	1152 sampling plots	240 gap plots

Gap Study

In summer 2000, we revisited 24 streams from the 1999 inventory, six from each study watershed, to sample vegetation in natural forest gaps caused by tree mortality, tree bole or branch snap, fluvial scouring, or hillslope failure. Since we noted considerable east to west variation in the riparian forests of each watershed, we stratified our sampling to select randomly two streams in the westernmost, middle, and easternmost sections of each study watershed. Beginning at the location of the 1999 hectare plot, we sampled the first 10 gaps we encountered along each. Naturally occurring gaps ranged in area from 12 m² to over 2000 m² with the majority between 100 m² and 500 m². In most cases, these gaps were contained within the original hectare plot, but we occasionally searched a slightly longer section of stream (up to 300 m) to locate ten gaps. We included gaps from streamside, terrace, and hillslope locations and on both sides of a stream. In all, we collected 240 gap samples, 60 in each study watershed. Within each gap, we randomly located a 40 m² circular sampling plot and collected vegetation and environmental data as described for the riparian inventory above.

We prepared a dataset of 240 forested sampling plots for the same 24 streams by subsampling from the riparian inventory dataset. First, we sorted all 18 sampling plots in each hectare plot by topographic classes in the riparian inventory, yielding six potential sampling plots in each class. Then we selected the three sites with highest overstory cover in each of the three topographic classes. Next, we randomly selected the next most densely vegetated plot from one of the three classes to yield a total of ten forest samples for each stream. Finally, we combined this dataset with the samples from the gap inventory to yield a gap-forest dataset of 480 sampling plots evenly split between gap and forest environments at 24 streams.

Gradient Quantification

Light. We developed an equation to predict understory light from canopy cover estimates for use with the 1999 riparian inventory. To do this, we took hemispherical photographs and sampled total cover and overstory cover at 120 sites in French Pete and Lookout Creeks in the Cascade Mountains using the methodology described above for the riparian inventory for the cover estimates. French Pete Creek has a relatively intact riparian forest, and Lookout Creek was severely disturbed by a debris flow in 1996. Together, the two streams spanned the complete riparian light gradient from open disturbed gravel flats to dense, mature coniferous forest. Photographs were taken using an 8 mm fish-eye lens on a Canon AE1 camera. The camera was leveled on a tripod at 1 m above the ground and oriented to magnetic north for each photograph. Images were scanned, digitized, and analyzed using *CANOPY* (Rich 1989). *CANOPY* calculates various measures of canopy geometry and indices of light penetration, including indirect and direct site factors. We used the indirect site factor as an estimate of biologically available radiation for understory plants, which we term Understory Light Index (ULI) for the rest of this paper. We did not adjust our estimates of ULI to reflect the estimated 10% difference in annual shortwave radiation from the cloudy coast (ca.

4350 MJ/m²) to the southern interior (ca. 4850 MJ/m²). Regression of ULI measurements on our ocular estimates of total cover produced the following equation ($R^2 = 0.70$, $P < 0.0001$) that we then used to make estimates of understory light index for the 1152 field plots from the riparian inventory.

$$(1) \text{ ULI} = (0.000033 * \text{Total Cover}^2 - 0.009 * \text{Total Cover} + 0.577) * 100$$

Moisture. In summer 2000, we selected a focal stream in each of the four 1999 study watersheds to evaluate moisture gradients. The focal stream in each watershed was subjectively chosen from the pool of sixteen streams in each study watershed based on accessibility and adequate tree regeneration for sampling of live seedlings. The focal streams were Mule Creek in the Applegate Watershed, Deadman Creek in the South Umpqua Watershed, McCrae Creek in the McKenzie Watershed, and Eckman Creek in the Alsea Watershed. We quantified moisture gradients in each watershed by measuring predawn plant moisture stress of reference conifer seedlings under 2 m in height along a topographic gradient from streamside to hillslope. Sampling was conducted in early to mid September. All conifer seedlings selected were healthy seedlings within 50 m of a stream horizontally and up to 20 m vertically. In most cases, we were able to locate 30 or more seedlings along a 200 m length of stream. Although we used *Pseudotsuga menziesii* (Mirbel) Franco seedlings wherever possible, we sampled seedlings of three additional native conifer species when it was absent: *Abies grandis* (Dougl.) Forbes, *Tsuga heterophylla* (Raf.) Sarg., and *Picea sitchensis* (Bong) Carr. For each seedling, we recorded its elevation above the stream and measured its predawn plant moisture stress using a pressure chamber (Waring and Cleary 1967) in mid September. Conifer seedlings were rare at less than 1 m above the stream in all watersheds, so where no conifers were found, we sampled riparian hardwood seedlings or shrubs of equivalent sizes at such locations, including *Fraxinus*

latifolia Benth., *Alnus rubra* Bong , *Physocarpus capitatus* (Pursh) Kuntze, and *Rubus spectabilis* Pursh.

Modeling Analyses

Because most climate variables we might have used were collinear across the study area, we developed a single integrated index of climatic favorability that functionally weights the seasonal influences of climate. To obtain this, we used a plant physiological process model, 3-PG (Physiological Principles Predicting Growth) (Landsberg and Waring 1997) to estimate gross primary productivity (GPP) in $\text{Mg C ha}^{-1} \text{ yr}^{-1}$ from climate data compiled for each hectare. We also used 3-PG to estimate maximum forest leaf area index (LAI) in m^2/m^2 at different sites on the climate gradient.

Like other process models, 3-PG first estimates the visible light (400-700 nm), designated as photosynthetically active radiation (ϕ_{pa}), which is assumed to be 50% of incoming short-wave radiation (ϕ_{s}). The actual amount of ϕ_{pa} utilized (ϕ_{pau}) is obtained by reducing the value of ϕ_{pa} by amounts determined by modifiers (dimensionless factors with values varying between zero and unity). The modifiers reflect constraints on radiation utilization imposed by partial to complete leaf stomatal closure associated with atmospheric vapor pressure deficits, frost, and drought. Drought effects are imposed by calculating a soil water balance, which is the difference between total monthly rainfall plus available soil water stored from the previous month, and transpiration, calculated using the Penman-Monteith equation with canopy stomatal conductance (G_{s}) modified by the vapor pressure deficit of the air, the availability of soil water, and the leaf area index (L) of the forest (Monteith 1965). Gross photosynthesis (P_{G}) is calculated by multiplying ϕ_{pau} by a maximum canopy quantum efficiency coefficient (α) that is a function of soil fertility. For these analyses, we assigned α equal to $0.05 \text{ mol C/mol photon}$ (2.74

g.C/MJ ϕ_{pau}).

We parameterized the model with climate data for each hectare plot obtained from DAYMET (Thornton et al. 1997) and set the fertility modifier at a constant setting of 0.5 and soil moisture storage at 300 mm before obtaining estimates of GPP for each hectare. Therefore, the variation in GPP estimates that we obtained from 3-PG was entirely climate-driven; areas with high GPP presented few climatic limitations to plant growth whereas areas with low GPP had one or more seasonal growth limitation.

We then ran the model with mean climate characteristics for our hectare plots in each study watershed at three classes of soil moisture availability that we thought might approximate conditions in different topographic positions in each watershed: (1) 1000 mm water (representing a low streamside terrace or seepage area with nearly unlimited moisture), (2) 300 mm (a floodplain site with deep soils and only minor seasonal moisture limitation); (3) 150 mm (a well drained hillslope or terrace site of moderate water holding capacity). We modeled canopy leaf area index in each watershed for each of these soil moisture classes to explore how it might be affected by climate and soil moisture availability. In addition, we applied a form of the Beer-Lambert Law to estimate the amount of light incident on the canopy that reaches the understory at each leaf area index value produced:

$$(2) \text{ Understory Light} = e^{-k \cdot \text{LAI}}$$

where k is an extinction coefficient and LAI is the leaf area index (m^2/m^2) predicted by 3-PG for the site. We selected a k value of 0.5, an intermediate value based on previously reported field studies in temperate forests (Marshall and Waring 1986, Bolstad and Gower 1990).

Data Analysis

We analyzed data from the riparian inventory at two scales. Richness of individual sampling plots in streamside, midslope, and hillslope subhabitats were the finest scale of analysis and considered to be estimates of local scale or alpha diversity. We also analyzed data at the hectare scale as estimates of stream reach scale diversity. In addition, by comparing compositional change from streamside to hillslope sampling plots in each hectare, we developed estimates of beta diversity for the hectare. For the statistical analyses, results, and discussion that follow, we will use terms alpha, beta, and hectare scale diversity to describe local scale (sampling plot) diversity, change from streamside to hillslope, and stream reach (hectare plot) scale diversity, respectively.

Statistical Summaries

We compiled statistical summaries of tree, shrub, and total woody plant species richness for each of three topographic positions at the local scale and at the hectare scale. We also tallied watershed scale richness by compiling a complete species list from the 16 hectare samples in each study watershed.

Controls on Species Richness. We used linear and quadratic stepwise multiple regression to determine the best univariate and multivariate models for alpha, beta, and hectare scale diversity. In all cases, variables were selected by maximum R^2 added and all variables retained were significant at the $p < 0.05$ level. Compared to linear models, quadratic regression added slightly to variance explained in many cases, but for ease of interpretation, we present only results from the linear models here.

For the analyses of alpha diversity, we used two landscape scale variables: (1) estimates of GPP at the hectare derived from the 3-PG model, and (2) logarithm of watershed area (LOGWA) as a proxy for stream power. Tree, shrub, and total

richness values and environmental variables (Table 3.2) were averaged for each of the six sampling plots in the three topographic classes within each hectare: (1) streamside, (2) midslope, and (3) hillslope environments. We then analyzed our data to determine the variables most predictive of alpha diversity for trees, shrubs, and total richness in each topographic setting. For analysis of hectare scale richness, we used GPP and LOGWA as above, but we averaged all environmental variables for the 18 sample plots in each hectare plot to give estimates of local environmental conditions in the hectare.

Beta Diversity. We calculated pairwise estimates of species turnover (beta diversity) between streamside and hillslope sampling plots in all six sampling cells of each the sixteen hectare plots in each study watershed using the formula of Wilson and Shmida (1984):

$$(3) \beta_T = [g(H) + l(H)]/2\alpha$$

Where $g(H)$ = species gained across a set of samples; $l(H)$ = species lost, and α = average sample richness.

We also calculated several estimates of the environmental heterogeneity across the plot pairs, including differences in litter depth, height above the stream, overstory cover, and ULI prior to analysis. We averaged all six beta diversity values for each hectare as well as values of the heterogeneity variables prior to statistical analysis.

We used stepwise multiple linear regression to determine the strongest predictors of beta diversity across the 64 hectares by analyzing beta diversity as a function of GPP, LOGWA, *Rubus spectabilis* cover, exposed rock, and the heterogeneity variables mentioned above.

Table 3.2. Environmental variables used in multiple regression analyses. Variables include: a) Landscape scale variables used in both hectare and sampling plot scale analyses, b) hectare scale summary variables used in the hectare scale analysis (mean values for all sampling plots (n=18) in the hectare, unless stated otherwise), c) sampling plot scale variables used in the sampling plot scale analysis, and d) variables used to analyze beta diversity.

a) LANDSCAPE SCALE

VARIABLE DEFINITIONS

VARIABLES

GPP	GROSS PRIMARY PRODUCTIVITY ($\text{Mg C ha}^{-1} \text{ yr}^{-1}$)
LOGWA	LOGARITHM OF WATERSHED AREA ABOVE HECTARE SITE

b) HECTARE SCALE

VARIABLES

BROWSE	UNGULATE BROWSING (ORDINAL 1-5 SCALE)
CLONAL	CLONAL SHRUB COVER(%)
CONCOVER	CONIFER COVER (%)
GEOM	GEOMORPHIC UNITS
LDEPTH	LITTER DEPTH(cm)
OCOV	OVERSTORY COVER(%)
ROCK	EXPOSED ROCK COVER (%)
RUSP	<i>Rubus spectabilis</i> COVER (%)
SCOUR	FLUVIAL SCOURING (ORDINAL SCALE 1-5)
SDEPTH	SOIL DEPTH(cm)
TCOV	TOTAL FOLIAR COVER(%)
TOPOGRAPHY	TOPOGRAPHIC RANGE IN HECTARE PLOT (m)

c) SAMPLING PLOT SCALE

VARIABLES

BROWSE	HERBIVORE BROWSING IN SAMPLING PLOT (ORDINAL 1-5 SCALE)
CLONAL	CLONAL SHRUB COVER IN SAMPLING PLOT (%)
CONCOVER	CONIFER COVER IN CANOPY LAYER (%)
HAS	SAMPLING PLOT HEIGHT ABOVE STREAM (m)
LDEPTH	LITTER DEPTH (cm)
OCOV	OVERSTORY COVER (%)
ROCK	EXPOSED ROCK COVER (%)
RUSP	<i>Rubus spectabilis</i> COVER (%)
SCOUR	FLUVIAL SCOURING (ORDINAL 1-5 SCALE)
SDEPTH	SOIL DEPTH (cm)
TOPOG	TOPOGRAPHIC RANGE IN PLOT (m)
ULI	UNDERSTORY LIGHT INDEX (%)

d) VARIABLES USED IN

ANALYSIS OF BETA DIVERSITY

ULI DIF	DIFFERENCE IN UNDERSTORY LIGHT (%) AMONG SAMPLING PLOTS
TOP DIF	DIFFERENCE IN HEIGHT ABOVE STREAM BETWEEN SAMPLING PLOTS
OCOV DIF	DIFFERENCE IN OVERSTORY COVER BETWEEN SAMPLING PLOTS
LDEPTH DIF	DIFFERENCE IN LITTER DEPTH BETWEEN SAMPLING PLOTS

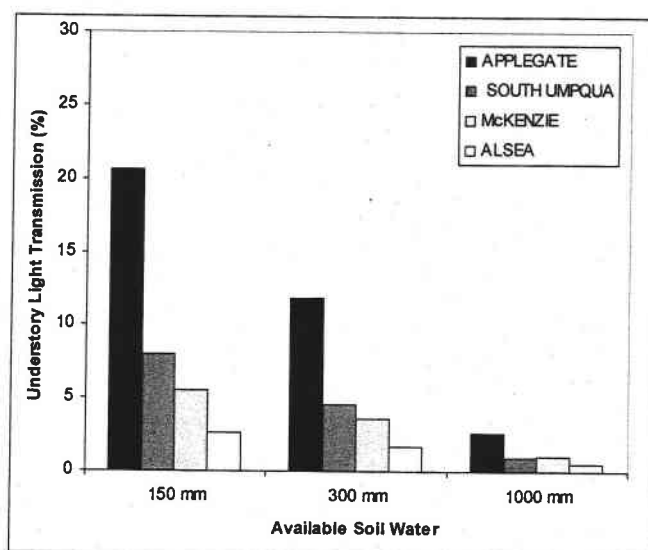
Effects of Gap Disturbance. We calculated species richness for gaps and adjacent forested areas at each of the 24 stream reaches in the gap inventory at three spatial scales: (1) the individual gap (analogous to the sampling plot) scale, (2) stream reach scale (10 gaps or 10 forest plots), (3) watershed scale (total from the 60 gap or 60 forest plots in each watershed). We used paired t-tests to evaluate the differences in richness of stream reach scale samples. Because individual gap samples and watershed summaries were pseudoreplicated and unreplicated, respectively, they were not analyzed statistically. We also plotted the difference in stream reach scale richness between gap and forest sites against GPP to evaluate our subhypothesis (3c) that the effect of gaps on richness is positively correlated with GPP.

RESULTS

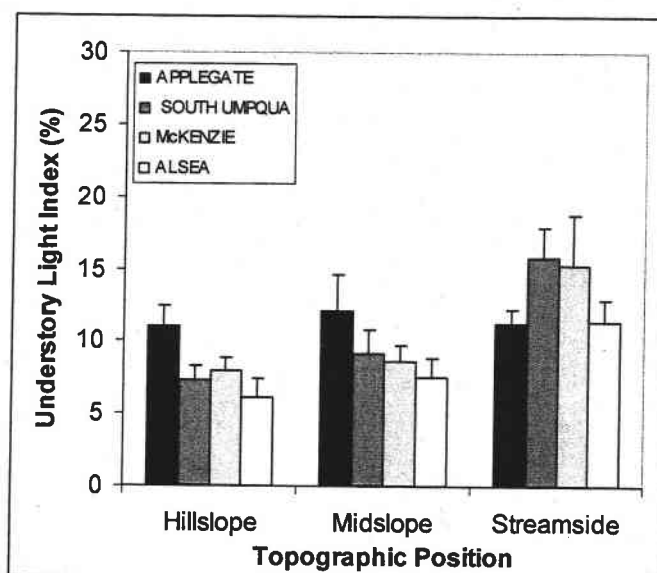
Statistical Summaries and Modeling Analyses

Watershed Scale Productivity and Gradient Structure

Modeled estimates of annual gross primary productivity nearly doubled from south to the north (mean \pm s.d. = 13.7 ± 1.2 , 16.9 ± 0.9 , 19.3 ± 1.5 , 24.5 ± 1.5 Mg C ha⁻¹ yr⁻¹ for sites in the Applegate, South Umpqua, McKenzie, and Alsea, respectively). Modeled LAI also increased from south to north at most levels of soil water availability. Estimates of LAI and understory light based on 3-PG suggested that sites with lowest levels of soil water (approximations of hillslope environments) would have greatest understory light in each watershed, and that the Applegate watershed would have substantially greater light at maximum LAI than the other three watersheds (Figure 3.3a). This light model prediction was partially at odds with field estimates of light at the local scale; understory light decreased



a.

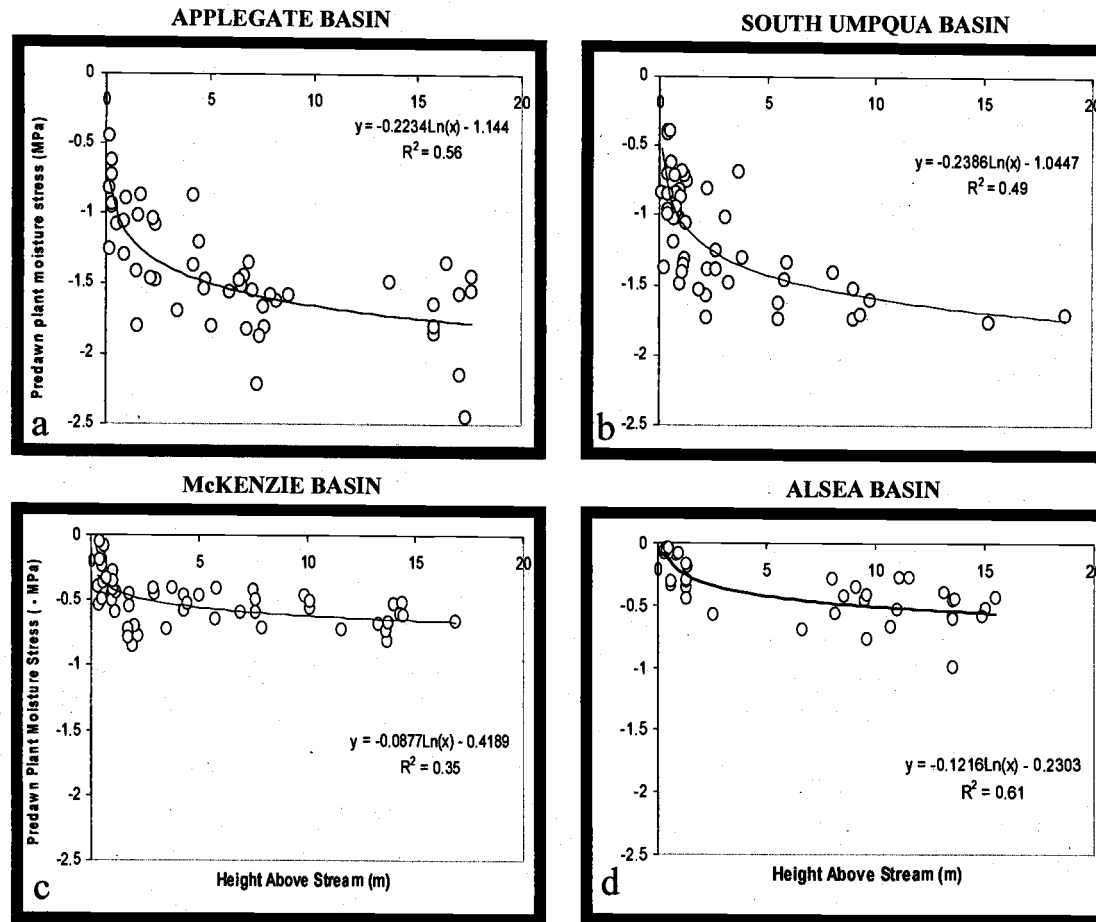


b.

Figure 3.3a,b. (a) Modeled understory light at three levels of available soil water (estimated to correspond with hillslope, midslope, and streamside topographic positions) in each of the four study watersheds. (b) Mean (+ s.e.) understory light estimates based on field sampling in each watershed at streamside, midslope, and hillslope sites (n=16 per topographic position per watershed).

towards hillslopes in three of the four watersheds (Figure 3.3b). Thus, near streamsides, fluvial disturbance and the stream canopy gap appeared to have greater influence on understory light availability than climatic influences on potential LAI. However, field-based estimates of understory light for midslope and hillslope environments were in general agreement with modeled estimates, suggesting understory light availability in those settings does decrease toward the wettest climates (Figure 3.3a, b). These findings are consistent with our Subhypothesis (3a) that understory light levels decline with increasing GPP across the region, but only at sites away from the immediate streamside.

Despite the fact that all four focal streams were perennial, the riparian forests in southwest Oregon showed a greater range in plant moisture stress across the streamside to hillslope topographic gradient than the northern forests (Figure 3.4a-d). Scatterplots of plant predawn water potentials (PMS) for all the streams showed a concave form with the most rapid decreases in water potential occurring in the first few meters of rise from the streamside. Curves for each stream appeared to approach a stream-specific asymptote in plant moisture stress with increasing elevation that probably represents a convergence with the upland moisture regime. For streams in southwest Oregon, PMS values were typically lower than -1.5 MPa at >10 m above the stream, whereas only one seedling was less than -1.0 MPa in the two northern watersheds. Streamside terraces of the Applegate focal stream, on average, had lower water potentials than hillslopes of the McKenzie and Alsea watershed streams (Figure 3.4a-d). These findings are consistent with our Subhypothesis (3b) that riparian forests in wet, productive climates have muted topographic moisture gradients relative to those in drier climates. Spring and summer (April 1 to September 5) precipitation totals for 2000 for Medford and Corvallis, climate stations that represent southwest and northwest Oregon, were 136.9% and 74.4% of 1971-2000 averages, respectively (Agrimet 2004, Western Regional Climate Center 2004). This suggests our findings of drier conditions in southwest Oregon are not anomalous, and probably conservative.



1
2 Figure 3.4 a-d. Scatterplots of predawn plant moisture stress (xylem pressure potential) in (MPa) for conifer seedlings and
3 streamside shrubs < 2 m tall as a function of height above the stream for focal streams in each study watershed, mid-September,
4 2000: (a) Applegate watershed, (b) South Umpqua watershed, (c) McKenzie watershed, (d) Alsea watershed.

Multiscale Patterns of Diversity

The four study watersheds showed substantial differences in woody plant richness at all scales. Total watershed scale richness was highest in the Applegate, the southern-most watershed, and declined steadily from south to north (71, 64, 58, and 47 species for the Applegate, South Umpqua, McKenzie, and Alsea, respectively). Hectare scale richness (mean \pm s.d.) showed a similar geographic pattern (33.6 ± 4.8 , 33.0 ± 4.7 , 29.6 ± 5.4 , 20.8 ± 5.2 , resp. Table 3.3). A map of the species richness of individual hectare plots (Figure 3.5) illustrates that high diversity plots were typically located in southwest Oregon, but also occurred in the eastern McKenzie watershed. At the scale of 40 m² sampling plots, topographic positions varied in species richness (Table 3.3). Woody species richness increased from streamsides to hillslopes in all watersheds except the Alsea, where richness did not vary by topographic position. The rankings of the watersheds for mean richness at each topographic position were largely the same as described for the hectare samples, except streamsides in the South Umpqua had slightly lower mean richness than streamsides in the McKenzie watershed. The richest local environments were hillslopes in the Applegate watershed (10.1 ± 3.2 species/40 m²) (mean \pm s.d.) whereas the poorest sites were terraces in the Alsea watershed (5.3 ± 2.0 species/40 m²).

Multiscale Controls on Species Diversity

Controls on Alpha Diversity

At the scale of sampling plots (40 m²), GPP was the variable most consistently selected in multiple linear regression models of species richness (Table 3.4). However, other local scale factors were also important. Near streams, stepwise multiple linear regression selected a multivariate model including GPP,

Table 3.3. Mean (\pm standard deviation (S.D.)) richness of trees, shrubs, and all woody plants in each study watershed at two scales: a.) hectare scale, b.) sampling plot (alpha) scale for streamside, midslope, and hillslope topographic positions.

SAMPLE SCALE	STUDY WATERSHED							
	Applegate		South Umpqua		Mckenzie		Alsea	
	Mean	(S.D.)	Mean	(S.D.)	Mean	(S.D.)	Mean	(S.D.)
a.) HECTARE SCALE								
Tree Richness	10.5	(1.6)	9.8	(1.0)	7.9	(1.7)	5.3	(1.6)
Shrub Richness	23.1	(4.2)	23.2	(4.2)	21.8	(4.3)	15.5	(4.1)
Total Richness	33.6	(4.8)	33.0	(4.7)	29.6	(5.4)	20.8	(5.2)
b.) SAMPLING PLOT SCALE								
Streamside								
Tree Richness	2.4	(1.2)	2.3	(1.5)	1.9	(1.6)	0.8	(0.8)
Shrub Richness	6.3	(2.8)	4.6	(2.3)	5.0	(2.2)	4.6	(1.8)
Total Richness	8.7	(3.3)	6.9	(3)	7.0	(3)	5.4	(2.1)
Midslope								
Tree Richness	2.6	(1.3)	2.4	(1.3)	2.0	(1.4)	0.6	(0.8)
Shrub Richness	6.9	(3.1)	6	(2.3)	5.8	(2.4)	4.7	(1.6)
Total Richness	9.5	(3.4)	8.4	(2.8)	7.8	(2.9)	5.3	(2)
Hillslope								
Tree Richness	3.1	(1.4)	2.4	(1.4)	2.0	(1.3)	0.7	(0.9)
Shrub Richness	7.1	(2.8)	6.7	(2.2)	6.0	(2.7)	4.7	(1.6)
Total Richness	10.1	(3.2)	9.1	(2.9)	8.0	(3.2)	5.4	(1.7)

fluvial scouring, and litter depth as best predictive model of total richness. At midslope and hillslope sites, GPP was negatively associated with richness of both trees and shrubs and was selected in every regression model chosen by stepwise

Table 3.4. Multivariate models selected by stepwise multiple regression for sampling plot (40 m²) scale richness (alpha diversity) of trees, shrub, and all woody species for streamside, midslope, and hillslope topographic classes. For each model, partial coefficients of determination (R² values) follow order of regression equation parameters from left to right. See Table 3.2 for variable definitions.

	Model Equation	Model R ²	F-Statistic	P > F
Streamside				
Tree Richness	3.12 - 0.071*(GPP) - 0.021*(RUSP) + 0.041*(LDEPTH)			
Partial R ²	0.38 0.06 0.04	0.48	18.2	< 0.001
Shrub Richness	9.98 - 0.00057*(ULI) - 0.124*(GPP) - 0.900*(SCOUR)			
Partial R ²	0.18 0.13 0.06	0.37	11.7	< 0.001
Total Richness	14.55 - 0.267*(GPP) - 0.000541*(ULI) - 0.626*(SCOUR)			
Partial R ²	0.34 0.12 0.04	0.50	19.3	< 0.001
Midslope				
Tree Richness	4.37 - 0.124*(GPP) - 0.015*(RUSP)			
Partial R ²	0.56 0.04	0.60	46.4	< 0.001
Shrub Richness	7.69 - 0.167*(GPP) + 0.335*(HAS)			
Partial R ²	0.22 0.10	0.32	13.8	< 0.001
Total Richness	13.346 - 0.3527*(GPP) + 0.257*(HAS)			
Partial R ²	0.50 0.03	0.53	34.6	< 0.001
Hillslope				
Tree Richness	5.03 - 0.163*(GPP) - 0.011*(CLONAL) + 0.046*(LDEPTH)			
Partial R ²	0.59 0.06 0.03	0.68	42.9	< 0.001
Shrub Richness	10.17 - 0.216*(GPP)			
Partial R ²	0.28	0.28	24.0	< 0.001
Total Richness	16.06 - 0.419*(GPP)			
Partial R ²	0.52	0.52	24.4	< 0.001

multiple regression. In general, relationships between GPP and richness and overall coefficients of determination were higher for trees than for shrubs, and intermediate for total richness (Table 3.4). In models of local richness of midslope sites, height above stream explained an additional 3% to 10% in variance over GPP alone. Overall, the results provided additional support for Subhypothesis 3a, that alpha diversity declines as GPP increases from dry to wet climates, coincident with

the decline in understory light. This effect was most evident away from the stream edge, where light availability was apparently more closely linked to climate (GPP) than to fluvial disturbance.

Controls on Beta Diversity

Presence of exposed rock, *R. spectabilis* cover, logarithm of watershed area, and variation in understory light across the floodplain were all significant terms in the final model selected by stepwise regression of beta diversity (Table 3.5a). All seemed to correspond with field observations of natural heterogeneity in these forests. First, exposed rock outcrops, which were most common in riparian forests of the South Umpqua and Applegate watersheds, often had lower vegetation cover and harbored islands of highly distinct xerophytic flora. Second, where *R. spectabilis* was abundant, we observed that the riparian forest was typically quite uniform in composition from streamside to hillslope. Third, the logarithm of watershed area and light variation were both positively associated with beta diversity and appeared to describe the increased heterogeneity caused by fluvial activity along larger streams. Floodplains along larger streams closely juxtaposed open, disturbed areas near the stream with dark, forested environments on midslopes and hillslopes; each of these environments supported distinctive species.

Multiple regression analyses did suggest that beta diversity declines from dry to wet climates, but the strong positive correlation ($r = 0.78$) between *R. spectabilis* cover and GPP complicated the evaluation of Subhypothesis 3b (lower beta diversity in wet climates). *R. spectabilis* cover was selected over GPP in the most explanatory regression model (Table 3.5a). However, when *R. spectabilis* was excluded from analysis, GPP was a significant term in the final multiple regression models. So it is difficult to differentiate the effects of *R. spectabilis* from the high GPP environments in which it is most abundant. The fact that regression models with *R. spectabilis* instead of GPP explained about 5% more

variance than GPP, suggest that the competitive influence of the shrub in these riparian forests creates more compositional uniformity than high GPP alone.

Controls on Hectare Scale Richness

Hectare scale diversity declined sharply from the driest climates to the wettest climates (Figure 3.5). GPP was the strongest predictor of hectare scale richness for both trees and shrubs in nonlinear models, and typically the first factor selected in stepwise multiple linear regression models, suggesting that climate is a more important control of diversity patterns than local variables alone (Hypothesis 1). The negative relationship between GPP and diversity in all models provided no support for Hypothesis 2 (species diversity is directly controlled by climate). Rather, it is most consistent with Hypothesis 3 (climate indirectly controls riparian plant diversity). From dry to wet climates there was a sharp increase in *R. spectabilis* cover, declines in understory light and in moisture heterogeneity, and decreases in both alpha and beta diversity within hectares. These climate-associated changes suggest intermediate mechanisms whereby climate drives decreases in hectare scale diversity from dry to the wet climates.

Stepwise multiple linear regression of hectare data also selected several other potentially important influences on hectare scale richness. The most powerful models for tree, shrub and total woody plant richness at the hectare scale included both GPP and *R. spectabilis* cover, as well as exposed rock, and logarithm of watershed area (Table 3.5a,b). The latter factors were also important in models of beta diversity. Moderate to strong correlations of alpha diversity and beta diversity with hectare scale diversity, ($r=0.70$ and $r=0.55$ for alpha and beta diversity respectively) suggest that the factors influencing these complementary dimensions of local diversity have additive effects on diversity at the hectare scale.

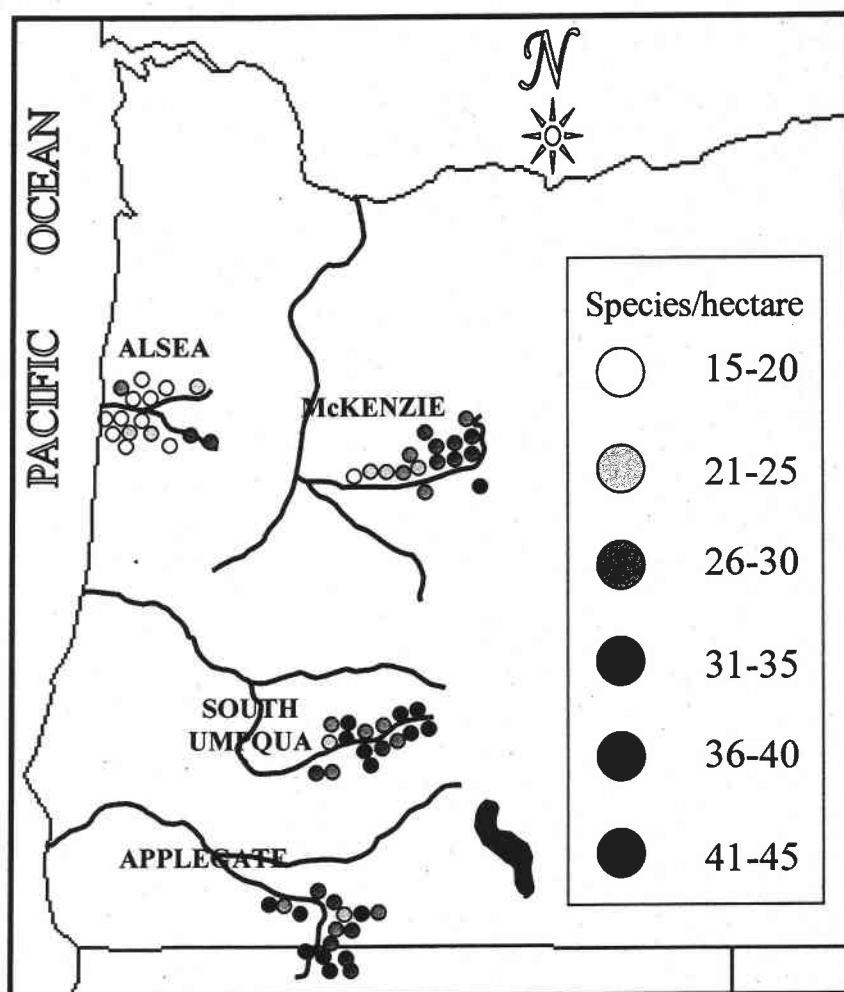


Figure 3.5 Map illustrating spatial pattern of woody species richness per hectare across the 64 sample reaches in the Alsea, McKenzie, South Umpqua, and Applegate watersheds.

Effects of Gap Disturbance

Across all watersheds, gap samples were typically richer in species than adjacent forest samples, but the magnitude of these differences varied by watershed (Table 3.6). The largest difference at a single stream was at Pipe Fork Creek in the Applegate watershed, where 10 gaps had 17 more species than the adjacent 10 forest samples. This creek is somewhat atypical for the Applegate in that it falls at the wetter western edge of the watershed and its floodplain is dominated by

Table 3.5a,b. Multivariate models selected by stepwise multiple regression for a.) beta diversity, and b.) hectare scale diversity. For each model, partial coefficients of determination (R^2 values) follow order of regression equation parameters from left to right.

a.) Beta Diversity

a.) Beta Diversity							
Model Equation				Model R ²	F-Statistic	P > F	
<hr/>							
Beta Diversity							
0.45 + 0.010*(ROCK) -0.0046*(RUSP) + 0.169*(LOGWA) + 0.00005*(ULI DIF)							
Partial R ²	0.28	0.12	0.10	0.06	0.56	8.6	0.001

b.) Hectare Scale Diversity

Model Equation					Model R ²	F-Statistic	P > F
Tree Richness							
12.31 - 0.501*(GPP) + 1.836*(LOGWA)							
Partial R ²	0.62	0.08			0.70	70.5	< 0.001
Shrub Richness							
29.87 - 0.580*(GPP) + 0.255*(ROCK)							
Partial R ²	0.35	0.14			0.49	29.0	< 0.001
Total Richness							
31.73 - 0.674*(GPP) - 0.119*(RUSP) + 3.241*(LOGWA) + 0.248*(ROCK)							
Partial R ²	0.50	0.12	0.05	0.03	0.70	33.4	< 0.001

Chamaecyparis lawsoniana (A. Murr.) Parl., a conifer that casts deep shade.

Elsewhere in the Applegate, within-forest richness was considerably higher and differences between gap and forest plots were smaller. In both Cascades watersheds, where *Tsuga heterophylla* often cast deep shade on floodplains, gaps showed a rather distinctive and decidedly richer flora than the dark forest understory. Gap environments of the Applegate yielded a rich species pool (56 species/0.24 ha), but the relatively open forest environments there had nearly as many species (52 species / 0.24 ha) (Table 3.6). In contrast, both gaps and forests of the Alsea were comparatively species poor environments. Differences between

Table 3.6 Mean tree, shrub and total species richness at sampling plot (individual gap), stream reach (total from 10 forest or gap plots at a site, approximately the hectare scale) and watershed (60 gap and forest samples) scales for the Alsea, McKenzie, South Umpqua, and Applegate watersheds. Standard deviations and results of paired one-sided t-test are provided at the stream reach scale. Statistical analyses are provided only for stream reach scale samples.

	STUDY WATERSHED			
	Applegate	South Umpqua	Mckenzie	Alsea
SAMPLING PLOT SCALE	Mean (S.D.)	Mean (S.D.)	Mean (S.D.)	Mean (S.D.)
Tree Richness				
GAP	3.4	3.4	2.1	0.7
FOREST	2.9	3.1	1.7	0.7
Shrub Richness				
GAP	7.4	7.3	6.3	5.1
FOREST	6.2	5.7	5.8	4.6
Total Richness				
GAP	10.7	10.7	8.4	5.8
FOREST	9.1	8.8	7.5	5.3
<u>REACH SCALE (10 GAPS)</u>				
Tree Richness				
GAP	9.0 (2.5)	8.3 (1.0)	6.5 (2.7)	3.3 (1.0)
FOREST	8.2 (2.2)	8.0 (1.1)	5.2 (1.3)	3.3 (1.8)
Paired one tailed t-test (n=6)	p = 0.21	p = 0.09	p = 0.05	p = 0.50
Shrub Richness				
GAP	20.0 (2.1)	22.2 (2.2)	17.7 (3.8)	14.0 (3.4)
FOREST	16.8 (4.0)	15.3 (2.7)	14.7 (3.8)	11.8 (1.7)
Paired one tailed t-test (n=6)	p = 0.08	p < 0.01	p < 0.01	p = 0.05
Total Richness				
GAP	29.0 (4.5)	30.5 (2.4)	24.2 (6.2)	17.3 (4.3)
FOREST	25.0 (5.4)	23.3 (3.1)	19.8 (4.5)	15.1 (3.0)
Paired one tailed t-test (n=6)	p = 0.11	p < 0.01	p < 0.01	p = 0.04
<u>WATERSHED SCALE (60 GAPS)</u>				
Tree Richness				
GAP	17	14	11	7
FOREST	17	10	9	8
Shrub Richness				
GAP	39	42	38	29
FOREST	35	34	29	21
Total Richness				
GAP	56	56	49	36
FOREST	52	44	38	29

gaps and forest environments were greatest in stream reach scale samples (10 gaps pooled for a stream) and total species pools, suggesting that although gaps are only slightly richer at the local scale, they accumulate species at a higher rate than adjacent forest environments when sample size increases.

We found little evidence to support our Subhypothesis (3c) that disturbance would have a greater effect on richness in more productive and competitive environments (Figure 3.6). The largest differences between gaps and forests were at relatively low levels of productivity, in the western Applegate and South Umpqua watersheds. Although these sites had greater contrasts between gaps and forests than the driest sites in the Applegate, they also showed much more difference than the most productive sites in the Alsea Watershed. At the highest productivity sites, *R. spectabilis* often strongly dominated gaps and diversity was low.

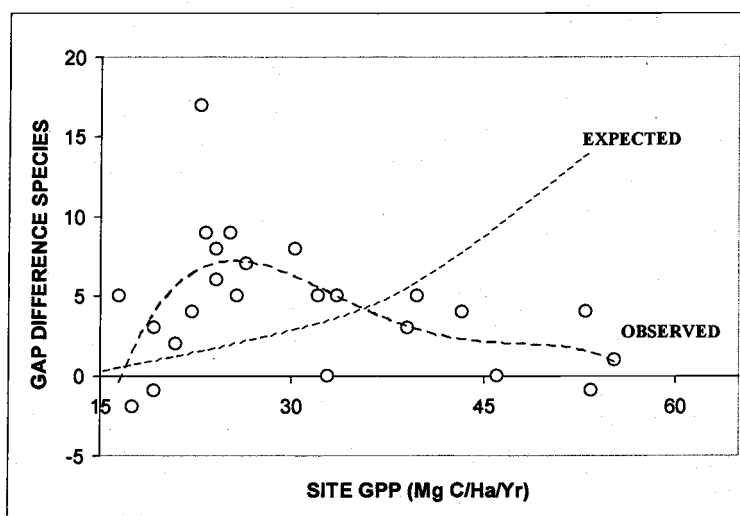


Figure 3.6. Relationship between modeled estimates of Gross Primary Productivity (GPP) and the gap difference (total species for 10 sampling plots in gap after subtracting total for 10 sampling plots in forest sites) in species for 24 streams in the four study watersheds. Hypothesized pattern is portrayed (EXPECTED) in comparison with field data (OBSERVED). Line of best fit for field data is from polynomial regression.

DISCUSSION

To develop a more integrative picture of the multiscale relationships influencing diversity, here we review patterns and analyses at each sample scale. Then we discuss findings in terms of our three primary hypotheses about controls on riparian plant species diversity.

Multiscale Controls on Species Diversity

Controls on Alpha Diversity

The influences of local and regional factors reached greatest parity in local environments near streamsides. Our finding that alpha diversity (i.e., sampling plot richness) was negatively associated with gross primary productivity is consistent with theory and other regional studies in upland forests of the region (Huston 1979, Waring et al. 2002). Alpha diversity, which is believed to be most strongly controlled by competition (Huston 1979, Sarr et al. in press), was lowest in high productivity environments, consistent with Subhypothesis 3a. These sites also had the lowest understory light levels (Figure 3.3b), as predicted. However, our findings that both GPP and *R. spectabilis* cover were better predictors of alpha diversity than understory light availability suggested that the competitive controls on diversity may involve more than simple light limitation.

Fluvial scouring near streamsides appeared to reduce alpha diversity, even in the relatively species rich landscapes of southwest Oregon (Tables 3.3, 3.4), suggesting that in those environments local factors can override climatic controls on richness. This provided partial support for Hypothesis 1 (local control of diversity).

Controls on Beta Diversity

Beta diversity across floodplains appeared to be controlled by a varied suite of factors, including local availability of shallow bedrock, variation in light and litter depth caused by fluvial disturbance, and the topographic moisture gradient. While streamsides were typically poorest in woody species, they had distinctive flood-tolerant and shade-intolerant species such as *P. trichocarpa* and *Salix* spp. that were seldom seen elsewhere and enriched the riparian forest. In a similar way, rocky areas often formed habitat islands for distinctive xerophytic species (e.g., *Ribes sanguineum* Pursh) that also increased hectare scale richness.

The effect of climate on beta diversity was less straightforward, but suggested by several field observations. First, we saw compelling evidence from our study of topographic moisture gradients (Figures 3.4 a-d) that moisture heterogeneity declines from dry to wet climates. Second, we noted that beta diversity declined at the highest levels of GPP (Table 3.5a). Third, a sharp rise in dominance by *R. spectabilis* and a decline in beta diversity in the coastal mountains suggest that the low moisture heterogeneity there allows the species to dominate throughout the riparian corridor. In the field, we observed that where *R. spectabilis* grows vigorously, it created thickets with relatively uniform floristic conditions, as noted by others (Pabst and Spies 1998). Our finding that beta diversity was more strongly associated with *R. spectabilis* cover than GPP presents the important, but rarely stated point that species turnover is linked as strongly to spatial patterns of dominance as it is to absolute resource heterogeneity.

Although we did not emphasize watershed processes in this study, we noted evidence that they also influence beta diversity. Stream reaches with larger contributing watersheds had greater levels of fluvial scouring and more distinctive riparian vegetation than smaller streams, as noted by other authors (Hupp 1986), and this floodplain differentiation was important for beta diversity across the streamside to hillslope gradient.

These findings are consistent with our Subhypothesis 3b that wetter climates would have lower moisture heterogeneity and beta diversity than forests in dry climates, but suggest that beta diversity is a complex phenomenon created by a variety of factors. These factors include variation in light, substrate conditions, moisture availability, and competitive dominance.

Effects of Gap Disturbance

Our field observations provided only partial support for our Subhypothesis (3c) that disturbance would have a disproportionately greater effect in more productive riparian forests (Table 3.6). Gaps in the Cascades typically showed greater diversity relative to the adjacent *T. heterophylla*-dominated forests than did gaps in the driest forests of the eastern Siskiyou Mountains, where within-forest richness was highest. This pattern provided additional evidence that light is indeed less limiting and diversity is higher in the driest forests, as we hypothesized (Subhypothesis 3a). However, our finding that overstory gaps were not very effective in increasing richness in the very productive forests of the Coast Range suggests that either competitive controls on richness are no stronger there than in less productive climates, or, that canopy gaps are ineffective disturbances where clonal shrub dominance is an important regulator of diversity. Some support for the latter alternative comes from a comparable study in southern Appalachian forests, where the authors found that experimental canopy gaps did not increase diversity where the shrub *Rhododendron maximum* L. was strongly dominant in the understory (Beckage et al. 2000).

Huston (1999b) suggested that in very high resource environments, rapid vegetation response quickly removes the imprint of all but the largest disturbances, and acts against the maintenance of environmental heterogeneity. In coastal forests, we found relatively small differences in species composition between streamsidess and hillslopes and between gap and forest samples, suggesting that

heterogeneity is indeed harder to maintain in productive, densely vegetated riparian landscapes.

Controls on Hectare Scale Richness

Multiple regression analyses illustrated the value of the climate variable GPP in explaining patterns of hectare scale diversity (Tables 3.4, 3.5a,b.); GPP was the principal variable selected in regression models and was strongly and negatively associated with hectare scale richness. This suggests that Hypothesis 1 (local control of diversity) is not a satisfactory or complete explanation of stream reach scale diversity patterns in these riparian forests. The finding that GPP was negatively associated with richness at all scales provided no evidence for Hypothesis 2 (direct climatic control of diversity); the most productive and physiologically favorable climates had the lowest diversity. These findings provided strongest support for Hypothesis 3, that climate indirectly controls woody plant richness in riparian forests. As noted above, we recorded evidence in support of two of our three subhypotheses of how climate might indirectly affect diversity.

Taken together, these results support a conceptual model of indirect climate effects upon the riparian environment. First, climate affects density of riparian vegetation and, consequently, the availability of understory light, a potentially important limiting resource in terrace and lower hillslope environments. Second, climate controls the distribution and vigor of potentially dominant species that structure the competitive environment in riparian forests. Collectively, these landscape level controls on the competitive environment appear to govern alpha diversity. Third, climate also appears to control the steepness of the topographic moisture gradient from streamside to hillslope, an important driver of beta diversity. These interactive mechanisms operate to lower stream reach scale diversity from the driest to wettest climate across our study area. This conceptual model fits well with a general diversity model proposed by del Moral and Fleming

(1979) that described a similar decline in plant diversity across an east to west climate transect in the Cascades of Washington state.

Our inability to detect evidence of direct climatic control on species diversity may have been due to the generally mesic and productive climate in our study area overall. The loss of several mesophytic species from the coast to the interior (e.g., *Picea sitchensis*, *Vaccinium ovatum*), and especially from the Cascades to the drier eastern Siskiyou Mountains (e.g., *Tsuga heterophylla*, *Thuja plicata*), was more than balanced by the addition of xerophytic species with southern or eastern affinities (e.g., *Pinus ponderosa* Dougl., *Quercus* spp., *Ceanothus* spp., *Arctostaphylos* spp.), yielding a richer riparian flora in the drier watersheds. However, our observation of slightly lower richness at the driest sites of the Applegate watershed suggest that direct climatic limitations may become more important in more arid climates, as noted in regional studies of upland environments (Richerson and Lum 1980, Harrison et al. 2000, Waring et al. 2002).

CONCLUSIONS

In this multiscale analysis of woody plant diversity in riparian forests, we recorded evidence for an indirect model of climatic control on richness. In support of this model, understory light and moisture heterogeneity decreased with increasing GPP, coincident with declines in alpha, beta, and hectare scale diversity. These findings suggest that the diversity declines often recorded from moderate to highly productive environments are linked to two synergistic mechanisms, an increase in competitive pressures, and a decline in heterogeneity. The decline in diversity with increasing climatic favorability that we noted suggests that competitive mechanisms can override direct climate models of diversity in highly productive riparian forests, at least at the scales we measured. Local gap

disturbances yielded slightly higher richness at most sites, but the magnitude of this effect was not a direct function of GPP.

In addition to the important effects of the climate gradient, we also saw evidence of local and watershed influences on both alpha and beta diversity in these forests. In particular, fluvial scouring appeared to be an important control on alpha diversity near streamsides. This study points toward an integrated conceptual model whereby landscape scale controls such as climate and watershed position complement and interact with local controls (i.e., vegetation structure, environmental gradients) to jointly govern woody plant diversity in riparian forests.

CHAPTER FOUR - RIPARIAN TREE REGENERATION IN WESTERN OREGON: THE ROLES OF LIFE HISTORY, ENVIRONMENTAL GRADIENTS, AND GAP DISTURBANCE

INTRODUCTION

In the Pacific Northwest, riparian forests contain a diversity of tree species and environments (Hawk and Zobel 1974, Fonda 1974, Minore and Weatherly 1994, Tabacchi et al. 1996, Pabst and Spies 1998, 1999, Dykaar and Wigington 2000, Johnson et al. 2000, Hibbs and Bower 2001). Although some riparian hardwoods are known to establish (hereafter regenerate) in response to stream processes (Fetherston et al. 1995, Dykaar and Wigington 2000, Johnson et al. 2000, Pabst and Spies 2002), the regeneration dynamics of most native riparian tree species are poorly understood. In this study, we explore relationships between environmental factors and regeneration patterns of nearly two dozen native tree species in western Oregon.

The regeneration environment in any riparian forest encompasses variation caused by environmental gradients and a variety of disturbances. Near stream margins, frequent flooding favors species with rapid juvenile growth, flexible stems, and tolerance of seasonally anaerobic soils. On higher floodplain terraces, interplant competition is a strong selective pressure. At upland edges of the riparian zone, seasonal drought is potentially important. Gap and fire disturbances also influence tree regeneration. The presence of unique substrates, such as nurse logs, is likely important for some Pacific Northwest trees (e.g., *Tsuga heterophylla* (Raf.) Sarg., *Picea sitchensis* (Bong) Carr.) (Pabst and Spies 1999). Larger scale gradients in conditions associated with topography and geography also affect the regeneration environment (Hupp 1986, Tabacchi et al. 1996, Montgomery 1999, Pabst and Spies 1999).

A functional understanding of species response to the regeneration environment requires a means to link species life history traits with environmental conditions. Seed size and tolerances of shade, drought, heat, and flood are attributes that often differentiate establishment of species along environmental or successional gradients (Huston and Smith 1987). Where several species share life history traits, they likely will show similar functional responses to their environment (i.e., regenerate in similar environments). Conceptual models of forest dynamics have often used functional group classifications to simplify the interpretation of plant species responses to environmental variation (Grubb 1977, Grime 1977, Whitmore 1989, Veblen 1992).

Many models of forest dynamics have emphasized the evolutionary importance of disturbance to distinguish adaptations among species (Grubb 1977, Whitmore 1989, Veblen 1992). Veblen (1992), for example, recognized continuous, gap-phase, and catastrophic "regeneration modes" to describe species adaptations to regenerate in closed forest conditions, and small and large disturbed areas, respectively.

Other models have integrated resource gradients as another axis for species specialization in heterogeneous environments (Grime 1977). Grime (1977) described competitive, ruderal, and stress tolerator strategies to describe plant specializations for dominance at resource rich sites, exploitation of disturbance at resource rich sites, and tolerance of resource poor sites, respectively.

In riparian forests, environmental gradients and disturbance undoubtedly both affect the tree species that become established. If so, it will be essential to explicitly link the effects of both of these factors with the life history traits of native tree species to construct a robust model of tree regeneration. Assuming that specific life history traits and environmental conditions coincide, such a model should be able to predict regeneration patterns for an array of species and environments.

STUDY OBJECTIVES

This paper describes two related and sequential analyses aimed at clarifying the regeneration needs of riparian trees across a diverse regeneration environment. In the first, we establish a foundation for predicting tree regeneration by classifying native tree species into functional groups and developing a model to interpret patterns of regeneration for each group. Next, we analyze field data to determine natural patterns of tree regeneration for each group in terms of environmental variables and gap disturbance and to evaluate the effectiveness and heuristic value of the regeneration model.

METHODS

Identification of Functional Groups Related to Riparian Tree Regeneration

We reviewed literature pertinent to the regeneration requirements for nearly two dozen riparian trees found in western Oregon riparian forests to help classify them into functional groups with potentially similar regeneration requirements. Minore (1979) provided a summary of many tree life history traits relevant to regeneration and included rankings for many traits. A number of other regional studies or databases provided additional information (Waring and Major 1964, Waring 1969, Zobel et al. 1976, Franklin and Dyrness 1988, Burns and Honkala 1990a,b, Minore and Weatherly 1994, Pabst and Spies 1999, USDA 2002).

From this information base, we selected seed size and tolerance to shade, drought, and flooding as traits potential affecting species regeneration patterns. In addition, because microclimate tolerance is highly relevant to seedling survival (see Gray and Spies 1997) but rarely quantified, we used fire tolerance rankings (USDA 2002) as a simple proxy for heat tolerance. We reasoned that the anatomical

characteristics (e.g., thick bark) that confer tolerance of cambial heating in older plants may correlate with tolerance of high soil surface temperatures (see Helgerson 1990) in seedlings.

For each of the five life history traits, we used the rankings from Minore (1979) and the other sources to score each species from 1 to 10 depending upon its tolerance relative to other species. For example, we scored *Taxus brevifolia* Nutt. and *T. heterophylla* a 10 for greatest shade tolerance, and *Populus trichocarpa* T. & G. 1 for least. These scores provided a set of semi-quantitative values with which to classify species' life history traits (Table 4.1).

We used Principle Components Analysis (PCA) in the multi-variate analysis package PC-Ord (McCune and Mefford 1999) to ordinate our species by the five life history traits and to guide the selection of functional groups (Figure 4.1). We used the default settings of PCA and the variance / covariance centered option.

The first two axes of the PCA ordination explained 87.4% of the variance in species characteristics. The first axis (Eigen value = 719.5, 68.3% variance explained) was positively correlated with flood tolerance (Eigen vector = 0.43) and negatively correlated with heat tolerance (Eigen vector = -0.57), drought tolerance (Eigen vector = -0.48) and seed size (Eigen vector = -0.43). The latter three characteristics were highly intercorrelated. We interpreted the PCA axis 1 as a gradient in drought and heat tolerance, and secondarily, flood tolerance among the species. The second axis (Eigen value = 201.5, 19.1% variance explained) was strongly correlated with shade tolerance (Eigen vector = 0.90), and secondarily with flood tolerance (Eigen vector = -0.27). Therefore, we interpreted PCA axis 2 as a gradient in shade tolerance. Species with low drought tolerance (high scores on PCA axis 1) separated strongly on PCA axis 2, with riparian hardwood species (*A. rubra*, *A. rhombifolia* and *P. trichocarpa*) receiving the lowest shade tolerance scores and drought intolerant conifers having the highest (Figure 4.1).

Table 4.1 Riparian tree species encountered in the four study watersheds, western Oregon, with four letter species codes, and functional group membership. Life history attributes are ranked from 1 (lowest tolerance or seed size) to 10 (highest) for each species.

FUNCTIONAL GROUP	SCIENTIFIC NAME	COMMON NAME	ORDINATION CODE	SHADE TOL.	FLOOD TOL.	HEAT TOL.	DROUGHT TOL.	SEED SIZE
1 <i>Alnus</i> Group	<i>Alnus rhombifolia</i> Nutt.	white alder	ALRH	2	9	2	1	1
	<i>Alnus rubra</i> Bong	red alder	ALRU	2	9	2	2	1
	<i>Populus trichocarpa</i> T. & G.	black cottonwood	POTR	1	10	1	1	1
2- <i>Tsuga</i> Group	<i>Picea sitchensis</i> (Bong) Carr	sitka spruce	PISI	8	8	1	3	4
	<i>Taxus brevifolia</i> Nutt.	Pacific yew	TABR	10	6	2	5	7
	<i>Thuja plicata</i> Donn	western redcedar	THPL	9	10	1	4	2
	<i>Tsuga heterophylla</i> (Raf.) Sarg.	western hemlock	TSHE	10	3	1	3	2
3- <i>Acer</i> Group	<i>Abies grandis</i> (Dougl.) Forbes	grand fir	ABGR	8	6	7	6	6
	<i>Acer glabrum</i> Torr.	douglas maple	ACGL	7	5	4	7	7
	<i>Acer macrophyllum</i> Pursh.	bigleaf maple	ACMA	7	5	6	6	7
	<i>Chamaecyparis lawsoniana</i> (A. Murr.) Parl.	Port Orford cedar	CHLA	7	8	7	4	4
	<i>Cornus nuttallii</i> Aud.	Pacific dogwood	CONU	7	6	5	5	7
	<i>Fraxinus latifolia</i> Benth.	Oregon ash	FRLA	6	10	2	5	7
	<i>Calocedrus decurrens</i> (Torr.) Florin.	incense cedar	CADE	5	5	7	9	6
4- <i>Pseudotsuga</i> Group	<i>Castanopsis chrysophylla</i> (Dougl.) DC	chinquapin	CACH	5	4	7	8	9
	<i>Pinus lambertiana</i> Dougl.	sugar pine	PILA	3	6	8	7	8
	<i>Pseudotsuga menziesii</i> (Mirbel) Franco	douglas-fir	PSME	5	2	8	8	6
	<i>Quercus chrysolepis</i> Liebm.	canyon live oak	QUCH	4	1	9	9	10
5- <i>Quercus</i> Group	<i>Arbutus menziesii</i> Pursh.	madrone	ARME	1	1	9	9	4
	<i>Pinus jeffreyi</i> Grev. & Balf.	jeffrey pine	PIJE	1	5	10	9.5	8
	<i>Pinus ponderosa</i> Dougl.	ponderosa pine	PIPO	1	6	10	9	8
	<i>Quercus garryana</i> Dougl.	Oregon oak	QUGA	1	1	10	9.5	10
	<i>Quercus kelloggii</i> Newberry	California black oak	QUKE	1	1	10	10	10

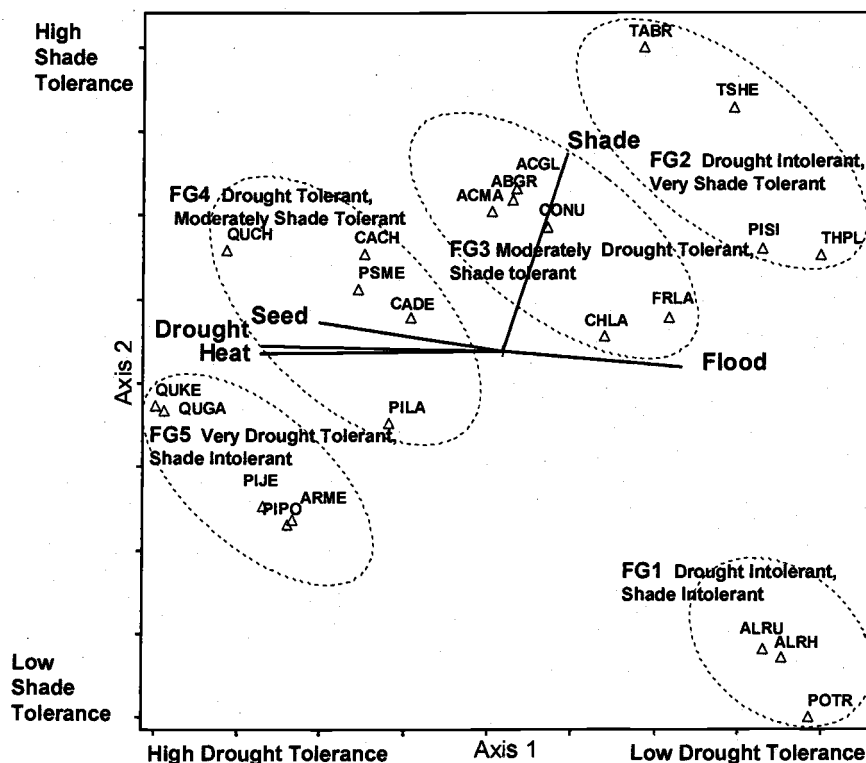


Figure 4.1 Ordination of riparian tree species (triangles) in two dimensional attribute space. Species names are provided for each code in Table 4.1. Vectors represent the five life history characteristics with length and coordinates proportional to the correlations with the ordination axes (Seed = seed size; Heat = heat tolerance, Drought = drought tolerance, Flood = flood tolerance; Shade = shade tolerance). Ellipses delineate functional groups: Functional Group 1 (FG1) Drought and Shade Intolerant (*Alnus* Group); FG2-Drought Intolerant Very Shade Tolerant (*Tsuga* Group); FG3-Moderately Drought Tolerant, Shade Tolerant (*Acer* Group); FG4-Drought Tolerant, Moderately Shade Tolerant (*Pseudotsuga* Group); FG5-Very Drought Tolerant, Shade Intolerant (*Quercus* Group).

We recognized five functional groups in the ordination space (Figure 4.1). Table 4.1 includes functional group membership for each of the 23 tree species. Each functional group is hereafter designated by its functional group abbreviation, and, for ease in interpretation, the generic name of the most common species in the group: Functional Group 1 (FG1), the *Alnus* Group, is a distinctive drought and

shade intolerant group of broadleaved deciduous riparian species. The species in Functional Groups 2-5 show trade offs in shade and drought tolerance; the most drought tolerant species have low shade tolerance and vice versa (Figure 4.1). Functional Group 2 (FG2), the *Tsuga* Group, is a drought intolerant, very shade tolerant group of coniferous species. Functional Group 3 (FG3), the *Acer* Group, is a moderately drought tolerant, shade tolerant group of broadleaved deciduous and coniferous species. Functional Group 4 (FG4), the *Pseudotsuga* Group, is composed of drought tolerant, moderately shade tolerant coniferous and broadleaved evergreen tree species. Lastly, Functional Group 5 (FG5), the *Quercus* Group, is a group of very drought tolerant, shade intolerant conifers (pines) and both broadleaved deciduous and evergreen trees. Three species, *P. sitchensis*, *Thuja plicata* Donn, and *Fraxinus latifolia* Benth., all have high reported flood tolerances, probably equal to the riparian hardwoods in the *Alnus* Group, yet all three have much greater reported shade tolerance than members of that group. Therefore, we did not separate these species from less flood tolerant species in their respective functional groups.

Development of the Life History / Context Model

To better understand and predict natural patterns of tree regeneration, we developed a model linking life history traits with environmental variation caused by climate and disturbance. Although climate and various disturbance types affect seedlings in many ways, we focus our attention on their effects on two aspects of a seedling's operational environment (*sensu* Mason and Langenheim 1957, Spomer 1973): microclimate and understory light availability. We will further narrow our discussion here by referring to the disturbance gradient as simply a categorical gradient in canopy cover from large open areas to smaller forest gaps to closed forest, irrespective of the causes of the canopy openings or other potential effects (e.g., soil disturbance).

Climate and disturbance have important and potentially interactive effects on the regeneration environment. Wetter climate zones of western Oregon develop taller forests, with greater maximum leaf areas and less understory light, than drier areas (Grier and Running 1977, Waring et al. 2002). Moreover, disturbed open areas in wet climates have lower solar radiation, vapor pressure deficits, and surface temperatures during the summer than open areas in drier climates (Waring and Running 1998). Summer field measurements in riparian forests indicated that total vegetation cover increases while surface temperatures, vapor pressure deficits, and soil drought decline from dry southwest to wet northwest Oregon (Chapter 3, Sarr and Hibbs unpublished data).

We propose that trade offs in drought and shade tolerance of forest species (described above) combined with our understanding of microclimate and light gradients will allow us to predict spatial patterns of regeneration for the different functional groups. The following assumptions about changes in microclimate and light across climatic and canopy cover gradients and functional group responses to these changes are used to develop regeneration domains for the different groups.

Climate and Canopy Cover Effects on the Regeneration Environment

(1) Microclimatic (drought, heat) stress will decrease from open environments toward smaller forest openings (gaps) or closed forests, and from the dry to wet climates, (2) maximum leaf area in undisturbed riparian forest will increase from the dry to the wet climates, resulting in a parallel decrease in understory light, (3) the contrast in microclimates between open areas and forest areas will decrease from the driest to the wettest climates.

Regeneration Responses to Climate and Canopy Cover Gradients

(4) Species regeneration in forest areas will shift from drought tolerant, less shade tolerant groups to drought intolerant, very shade tolerant groups from the dry to wet climates, (5) among shade intolerant species, regeneration in gaps or open environments will shift from drought tolerant to drought intolerant groups from the dry to wet climates, (6) less shade tolerant species will regenerate at highest levels in open environments, with the dependence of these species on forest openings becoming greatest in the wettest climates, (7) less drought tolerant, but more shade tolerant species will regenerate under a protective forest canopy in all except the wettest climates, where forest interiors are most light-limited and microclimates in openings are mildest, (8) the general patterns of tree regeneration abundances across climate and canopy cover gradients will reflect the reported drought and shade tolerance rankings of the species.

We developed a model that graphically integrates these assumptions, descriptively called the life history-context regeneration model. The model portrays the changes in local environmental conditions (microclimate, maximum leaf area, and understory light) across a macroclimate gradient from hot, dry interior to cool, wet coastal areas (Figure 4.2a). The positive relationship between macroclimate and maximum leaf area index in Figure 4.2a is based on empirical relationships developed by Grier and Running (1977). Regeneration domains for each functional group are presented as zones in the microclimate and understory light space where species in the group are well suited to the ambient levels of microclimatic and understory light conditions present (Figure 4.2a).

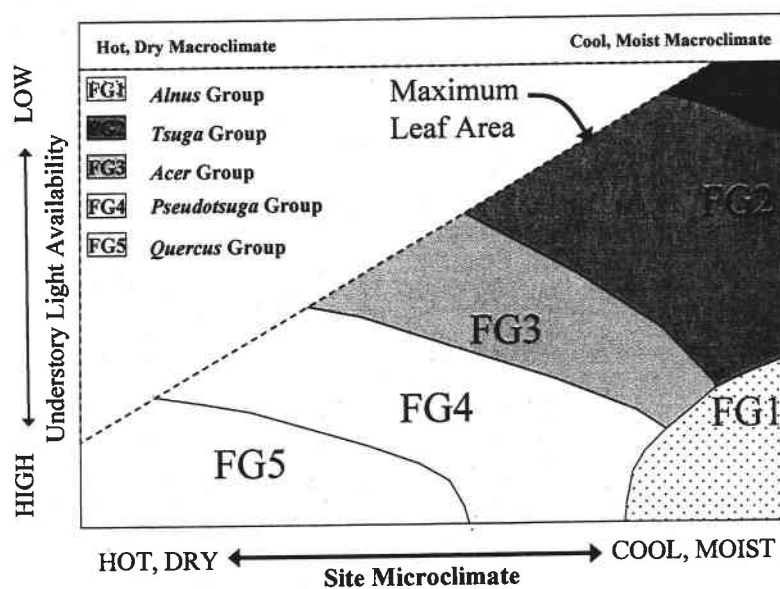
Shifts in regeneration environment conditions associated with disturbance-mediated reduction of canopy cover add another predictive element to the model. These changes can be illustrated as directional shifts in the environmental space of the regeneration model (Figure 4.2b). By overlaying a categorical gradient in canopy cover associated with disturbance, we show a range in regeneration environments

(i.e., open, gap, forest understory) in each of four different climatic subregions spanning the macroclimate gradient (Figure 4.2b). In all four subregions, the change in local conditions from open areas to gaps and forest is associated with a movement up and to the right in the gradient space (i.e., from warmest, driest, and brightest to the coolest, wettest, and darkest conditions available). The model illustrates that the absolute changes in understory light availability along the canopy cover gradient (vertical shift on light/leaf area index axis from open to forested areas) are greatest in the wet macroclimate of the Coast Range, whereas the changes in microclimate (horizontal shift on microclimate axis) are greatest in the hot, dry macroclimate of the eastern Siskiyou (Figure 4.2b).

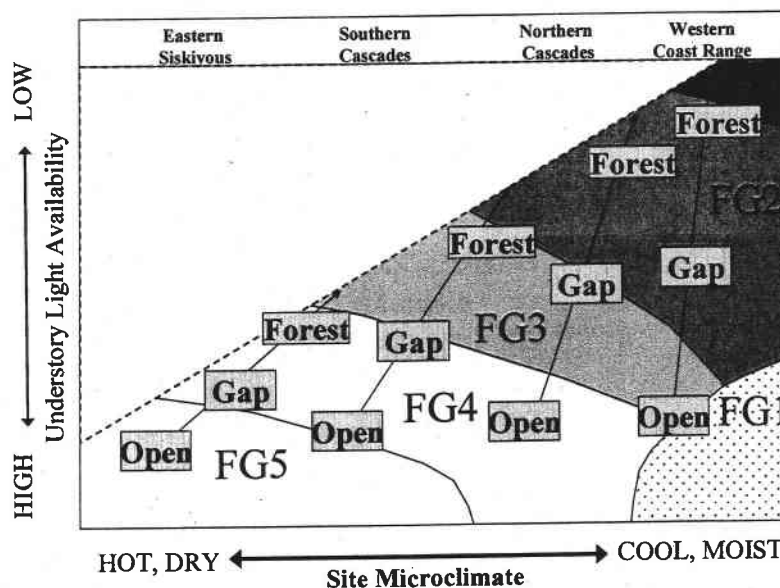
Taken together, these environmental changes are predicted to cause important shifts in the species favored at different points in the environmental space. For example, species in the drought intolerant, shade intolerant FG1 (*Alnus* Group) are limited to the only zone where both moisture and light are abundant (Fig. 4.2a,b). All other groups are predicted to show shifts in association with disturbance, due to macroclimate-driven changes in understory light and microclimate and tradeoffs between drought and shade tolerance. For example, the regeneration domain for drought intolerant, very shade tolerant FG2 (*Tsuga* Group) includes a wide portion of the light gradient in cool, wet climates, but is confined to sheltered forest settings in hot, dry climates (Figure 4.2a,b). The regeneration domain for the drought tolerant, moderately shade tolerant FG4 (*Pseudotsuga* Group), shows the opposite pattern, including a large range of regeneration environments in the driest climates but only forest openings in wetter climates.

Field Sampling

In 1999 and 2000, we sampled riparian vegetation in four watersheds of western Oregon chosen to sample the steep climate gradient (warm, dry south to cool, wet north) across western Oregon: (1) the Applegate in the eastern Siskiyou



a.)



b.)

Figure 4.2 a,b. a.) *Life history-context regeneration model* displaying optimal regeneration domains for each functional group in a two dimensional space of microclimate and understory light availability. The model illustrates the range of microclimates available for riparian tree regeneration across a macroclimate gradient. b.) The model with canopy cover gradients (i.e., open, gap, forest) overlaid for four climatic ecoregions of western Oregon. See the text for further explanation and examples.

Mountains; (2) the South Umpqua in the southern Cascades; (3) the McKenzie in the northern Cascades, and (4) the Alsea in the western Coast Range (Figure 4.3). The climatic moisture gradient is well expressed in summer vapor pressure deficits calculated for the four watersheds from the temperature-based method of Running et al. (1987) (mean (\pm s.d.) = 14.7 (\pm 1.2), 14.0 (\pm 0.9), 11.8 (\pm 0.9), 8.6 (\pm 1.2) millibars, for the Applegate, South Umpqua, McKenzie, and Alsea watersheds, respectively). The study sites in the McKenzie watershed had fewer growing degree days (base 0° C, data derived from DAYMET model of Thornton et al. 1997) than the other three watersheds (mean (\pm s.d.) = 3750 (\pm 263), 3672 (\pm 189), 3140 (\pm 237), and 3961 (\pm 117) growing degree days, for the Applegate, South Umpqua, McKenzie, and Alsea watersheds, respectively). The high number of growing degree days in the Alsea watershed reflects a long growing season; it is the coolest and cloudiest of the watersheds in summer.

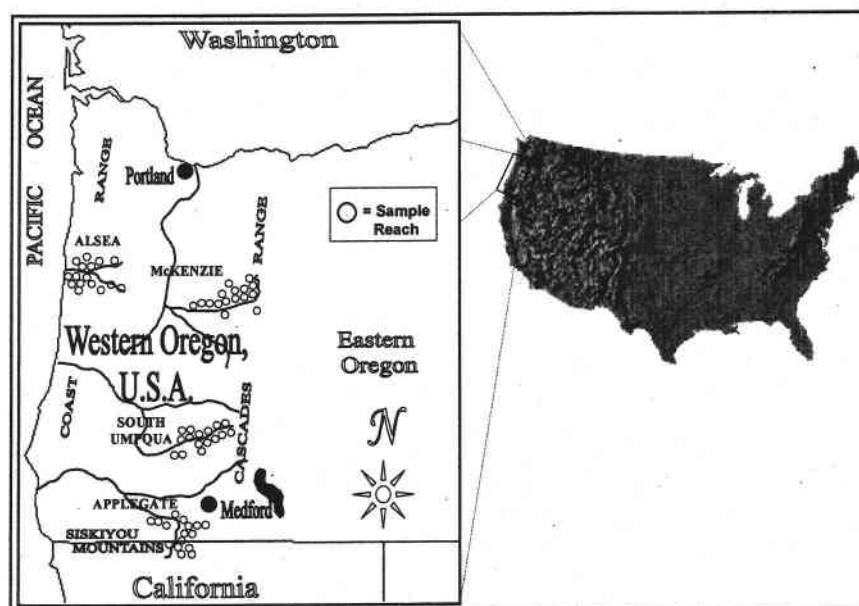


Figure 4.3. Map of study area and location of study watersheds and study sites. Triangles denote major regional cities.

We explored regeneration patterns in riparian forests of the four watersheds in two related field studies: (1) a broad riparian inventory of 64 1-ha riparian forest sites; (2) a gap study using paired comparisons of regeneration in gaps and forest interiors along 24 streams, six in each watershed.

Riparian Inventory

In 1999, we sampled riparian tree regeneration and environmental characteristics at sixteen 1st through 5th order stream reaches in each of the four study watersheds. Stream order and watershed area were determined for each stream at the sample reach from USGS 1:24,000 topographic quadrangle maps. For each watershed, we interviewed staff at the appropriate land management agency (USDA Forest Service or USDI Bureau of Land Management) to determine management histories of each potential sample reach. We then confined field sampling to stream reaches that had not had timber harvest or other management within the last 30 years and which occurred within 1 hour hiking distance (3-4 km) of an access road or trail. In each watershed, this yielded 30-50 potential sample reaches. Sample reaches were assigned numbers and sixteen numbers were selected at random for field sampling sites in each watershed (64 total). All plots were placed at least 50 meters upstream or downstream from a road or trail crossing and then a random distance from zero to 200 m further upstream or downstream. Although the distribution of stream orders differed substantially between the study watersheds, most sample streams selected in each (56 % – 94%) were second or third order streams.

At each sample reach, we established a plot that straddled the stream and was 200 m long by 50 m wide, not including the stream channel, thereby encompassing a hectare of riparian forest habitat (Figure 4.4). We will refer to this plot as the hectare plot. All distances were slope distances measured along the ground surface with a fiberglass tape.

Within each plot, we established 12 subplots of 25 x 33.3 m with the 33.3 m side parallel to the stream. The two subplots directly across the stream from each other were considered a pair. We randomly selected one subplot of each pair for sampling of vegetation and environmental characteristics. We divided the subplot to produce three contiguous 8 x 33.3 m sampling cells at increasing distances from the stream edge and then placed three sampling plots randomly ($4 \times 10 \text{ m} = 40 \text{ m}^2$, the long side parallel to the stream) in each subplot with one sampling plot per sampling cell. Presence and abundance of all tree seedlings (trees under 1.4 m tall) were characterized in each sampling plot. We counted seedlings on logs and on the ground for each species. Additional environmental data were collected in sampling plots.

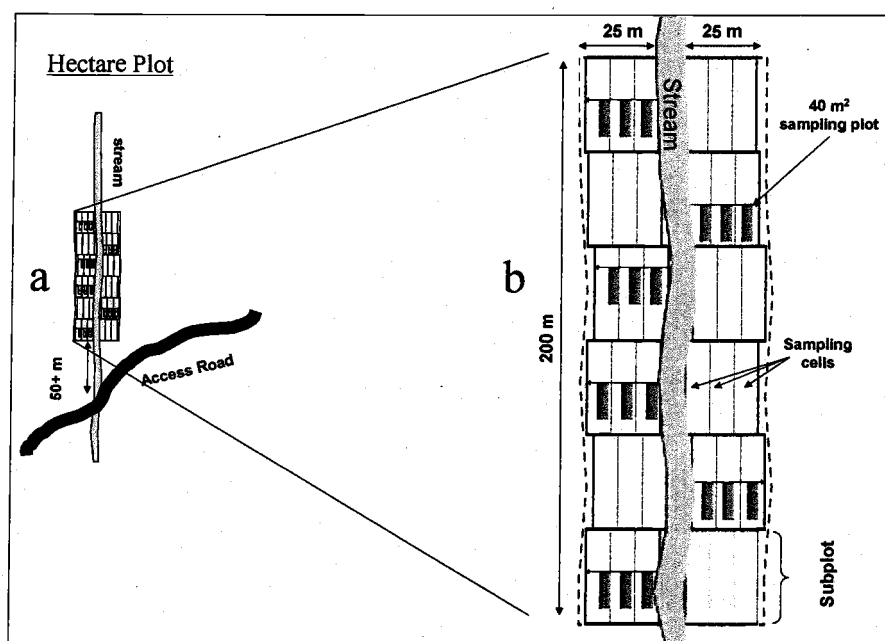


Figure 4.4. Diagram illustrating the location of: (a) the hectare plot relative to an access road and sample stream, and (b) the arrangement of the subplots, sampling cells and 40 m^2 sampling plots within the hectare plot.

Along these mountain streams, the three sampling plots in a subplot usually corresponded with a horizontal and vertical gradient from (1) streamside bars to (2) midslopes/flood plain terraces and (3) lower hillslopes. Although the placement of plots varied somewhat with respect to the morphology of the valley floor along a particular stream, we will refer to the three topographic positions as (1) streamside, (2) midslope, and (3) hillslope plots.

Ground distance from the sampling plot center to the current water's edge was recorded, and slope in degrees from the sampling plot center to the stream edge was estimated using a clinometer held at 1 meter above the ground. Slope data were used to compute height above stream and to develop slope-corrected estimates of plot areas. All seedling densities given use slope-corrected area. Overstory cover was an ocular estimate of tree cover straight up from a point 1.75 m above the ground viewed through a 20 cm diameter ring held vertically at arms length (ca. 45 cm). Total cover was estimated by applying the same method with the observer seated and included any shrub layers greater than 1.2 m above the ground, in addition to overstory cover.

Soil characteristics were determined by digging a 30 cm soil pit in the middle of each sampling plot. Litter depth and, where a bedrock layer was encountered, depth to bedrock, were measured. Where a bedrock layer was not encountered, an estimate of 35 cm was recorded.

We also recorded two indices of disturbance in each sampling plot. An index of fluvial scouring was defined as the proportion of each sampling plot that was visibly affected by fluvial activity, including obvious signs of fluvial erosion or deposition or flow channels. In a similar way, we recorded presence of herbivory by noting percent of sampling plot with browsing of shrubs and trees. In both cases, the index scores were: (1) disturbance noted in 0-20 percent of sampling plot, (2) 20-40 percent, (3) 40-60 percent, (4) 60-80 percent, and (5) 80-100 percent.

Gap Study

In summer 2000, we revisited 24 streams from the 1999 inventory, six from each study watershed, to sample vegetation in natural forest gaps caused by tree mortality, tree bole or branch snap, fluvial scouring, or hillslope failure. Because we noted considerable east to west variation in the riparian forests of each watershed, we stratified our sampling to select randomly two streams in the westernmost, middle, and easternmost sections of each study watershed. Beginning at the location of the 1999 hectare plot, we sampled the first 10 gaps we encountered along each. Naturally occurring gaps ranged in area from 12 m² to over 2000 m² with the majority between 100 m² and 500 m². In most cases, these gaps were contained within the original hectare plot, but we occasionally searched a slightly longer section of stream (up to 300 m) to locate ten gaps. We included gaps from streamside, terrace, and hillslope locations and on both sides of a stream. In all, we collected 240 gap samples, 60 in each study watershed. Within each gap, we randomly located a 40 m² circular sampling plot and collected tree regeneration and environmental data as described for the riparian inventory above.

We prepared a matching dataset of 240 forested sampling plots for the same 24 streams by subsampling from the riparian inventory dataset. First, we sorted all 18 sampling plots in each hectare plot by topographic classes in the riparian inventory, yielding six potential sampling plots in each class. Then we selected the three sites with highest overstory cover in each of the three topographic classes. We then randomly selected the next most densely vegetated plot from one of the three classes to yield a total of ten forest samples for each stream. Finally, we combined this dataset with the samples from the gap inventory to yield a gap-forest dataset of 480 sampling plots evenly split between gap and forest environments at 24 streams.

Data Analysis

Identifying Topographic and Geographic Patterns in Seedling Frequencies

We constructed a series of graphs for all the functional groups to illustrate broad scale patterns in seedling frequencies in each of three topographic classes: (1) streamside; (2) midslope; and (3) hillslope in each of the four study watersheds. In addition, we tabulated species abundances in each topographic and geographic setting and calculated seedling species richness for each functional group in each watershed.

Linking Environmental Factors to Tree Regeneration

We performed classification and regression tree (CART) analysis (Brieman et al. 1984) of log-transformed seedling counts using the statistical package SYSTAT (10.2). We chose CART over regression methods because it accommodates non-normal seedling data and different types of independent variables. The tree models generated by CART analysis provided simple, descriptive summaries of the factors associated with high and low abundances, and the hierarchical relationships among multiple factors. Explanatory power of splitting variables is presented as proportional reduction in error (PRE), which is analogous to the coefficient of determination (R^2) in multiple regression models.

Prior to CART analysis, we averaged environmental data and summed seedlings counts for the six 40 m² sampling plots in the three topographic classes for each of our 64 hectare plots, yielding 192 aggregate sample units. Because topographic units were nested in each hectare plot and not independent, we did not test relationships for significance. In all cases, we set the stopping settings in CART to select terminal nodes with at least 10 aggregate samples and to incorporate only splitting variables that yielded a proportional reduction in error of at least 0.05. We ran all analyses with log-transformed seedling abundances to

minimize the effect of extreme values on tree formation. To ease interpretation, we back-transformed the log-transformed seedling means and displayed median seedling abundances as seedlings/hectare for each terminal node in the regression tree. A complete list of variables used in CART analysis is provided in Table 4.2.

Table 4.2. Environmental variables used in classification and regression tree (CART) analyses. Variables include: a) Landscape scale variables, b) Sampling plot scale variables.

a) LANDSCAPE SCALE	
VARIABLES	VARIABLE DEFINITIONS
GDDTOT	GROWING DEGREE DAYS (0 ° C BASE)
VPDSUM	MEAN VAPOR PRESSURE DEFICIT JUNE-SEPTEMBER (mb)
LOGWA	LOGARITHM OF WATERSHED AREA (Ha) UPSTREAM OF HECTARE SITE
b) SAMPLING PLOT SCALE	
VARIABLES	
BROWSE	HERBIVORE BROWSING IN SAMPLING PLOT (ORDINAL 1-5 SCALE)
LWDVOL	LARGE WOODY DEBRIS VOLUME (m ³ /ha)
CLONAL	CLONAL SHRUB COVER IN SAMPLING PLOT (%)
CONCOVER	CONIFER COVER IN CANOPY LAYER (%)
HAS	SAMPLING PLOT HEIGHT ABOVE STREAM (m)
LDEPTH	LITTER DEPTH (cm)
OCOV	OVERSTORY COVER (%)
ROCK	EXPOSED ROCK COVER (%)
RUSP	<i>Rubus spectabilis</i> COVER (%)
SCOUR	FLUVIAL SCOURING (ORDINAL 1-5 SCALE)
SDEPTH	SOIL DEPTH (cm)
ULI	UNDERSTORY LIGHT INDEX (%)

Testing the Regeneration Model

We evaluated our life history / context regeneration model using the gap dataset. We assumed that the study watersheds presented a categorical climate gradient, whereas gaps and forest sites presented part of the categorical disturbance gradient. These conditions allowed us to partially test the regeneration model. From Figure 4.2b, we generated a table (Appendix 4.1) of 18 expected outcomes for

pairwise intra-watershed (gap vs. forest) and inter-watershed (e.g., Applegate gap vs. gap McKenzie gap) comparisons of seedling abundances in each functional group. We did not compare gaps in one watershed with forests in another, nor did we compare seedling abundance among functional groups. We compared seedling abundances between pairs of sites (e.g., gap vs. forest plots in Applegate watershed) and used the nonparametric chi-squared test to evaluate statistical significance of our predictions for each functional group and for all comparisons.

RESULTS

Geographic and Topographic Patterns of Riparian Tree Regeneration

We recorded strong shifts in composition, frequency, and abundance of tree regeneration from southwest to northwest Oregon (Applegate, South Umpqua, McKenzie, and Alsea watersheds, respectively; hereafter we describe geographic variation along this gradient Figure 4.4). The frequency of regenerating trees in sampling plots decreased south to north. Frequency was 82.3%, 70.1%, 57.6%, and 14.9%, respectively, in the 4 watersheds, while the number of species recorded in each was 17, 16, 11, and 8 (Figure 4.4f). Sharp local contrasts also occurred. Streamsides and terraces in the Alsea watershed, for instance, showed the highest and lowest mean seedling abundances, respectively, of all environments sampled (Table 4.3). We recorded *A. rubra* seedlings densities of up to 50 individuals / m² on streamside gravel bars of the Alsea watershed; adjacent terraces had none. *T. heterophylla* also showed aggregated regeneration, reaching high seedling densities on nurse logs (> 20 individuals/m²).

Functional Group Patterns

Seedlings of FG1 (*Alnus* Group) were most frequent and abundant near streams in all four watersheds, but with substantial regeneration away from the stream in the wettest watershed (Figure 4.5a, Table 4.3). As noted above, we recorded no seedlings on terraces in the Alsea, but observed seedlings at both streamside and hillslope sites. *Rubus spectabilis* (Pursh.) cover was typically greatest on terraces and may have limited establishment of this group of species. In contrast to alders (*Alnus* spp.) which were relatively common along all streams in the region, we saw relatively few *P. trichocarpa* seedlings at our study sites. Those we saw were primarily in open, very disturbed areas.

Abundances for FG2 (*Tsuga* Group) were highest in the Cascades, where the group, especially *Tsuga heterophylla*, composed the majority of all tree regeneration (Figure 4.5b). In the Alsea watershed, regeneration was relatively sparse; and *T. brevifolia* seedlings were not recorded. *T. heterophylla* and *T. plicata* were absent from the Applegate watershed. *P. sitchensis* occurred only within 10 km of the coast.

After *A. macrophyllum*, *Abies grandis* (Dougl.) Forbes was the most frequently regenerating species of FG3 (*Acer* Group) (Table 4.3). Trees in this group showed a pronounced decline in frequency and abundance from south to north. These species were most frequent close to streams in the Applegate and McKenzie watersheds and rarest on terraces in the Alsea watershed (Figure 4.5c).

FG4 (*Pseudotsuga* Group) species regenerated most frequently in the two southern watersheds (Figure 4.5d, Table 4.3). *P. menziesii* and *Castanopsis chrysophylla* (Dougl.) DC.) regenerated in all four watersheds, but were much more abundant in the south (Table 4.3). *Quercus chrysolepis* Liebm. was the most common tree regenerating in the Applegate watershed, but was absent elsewhere (Table 4.3). *Pinus lambertiana* Dougl. and *Calocedrus decurrens* (Torr.) Florin regenerated sporadically in all three interior watersheds (Table 4.3).

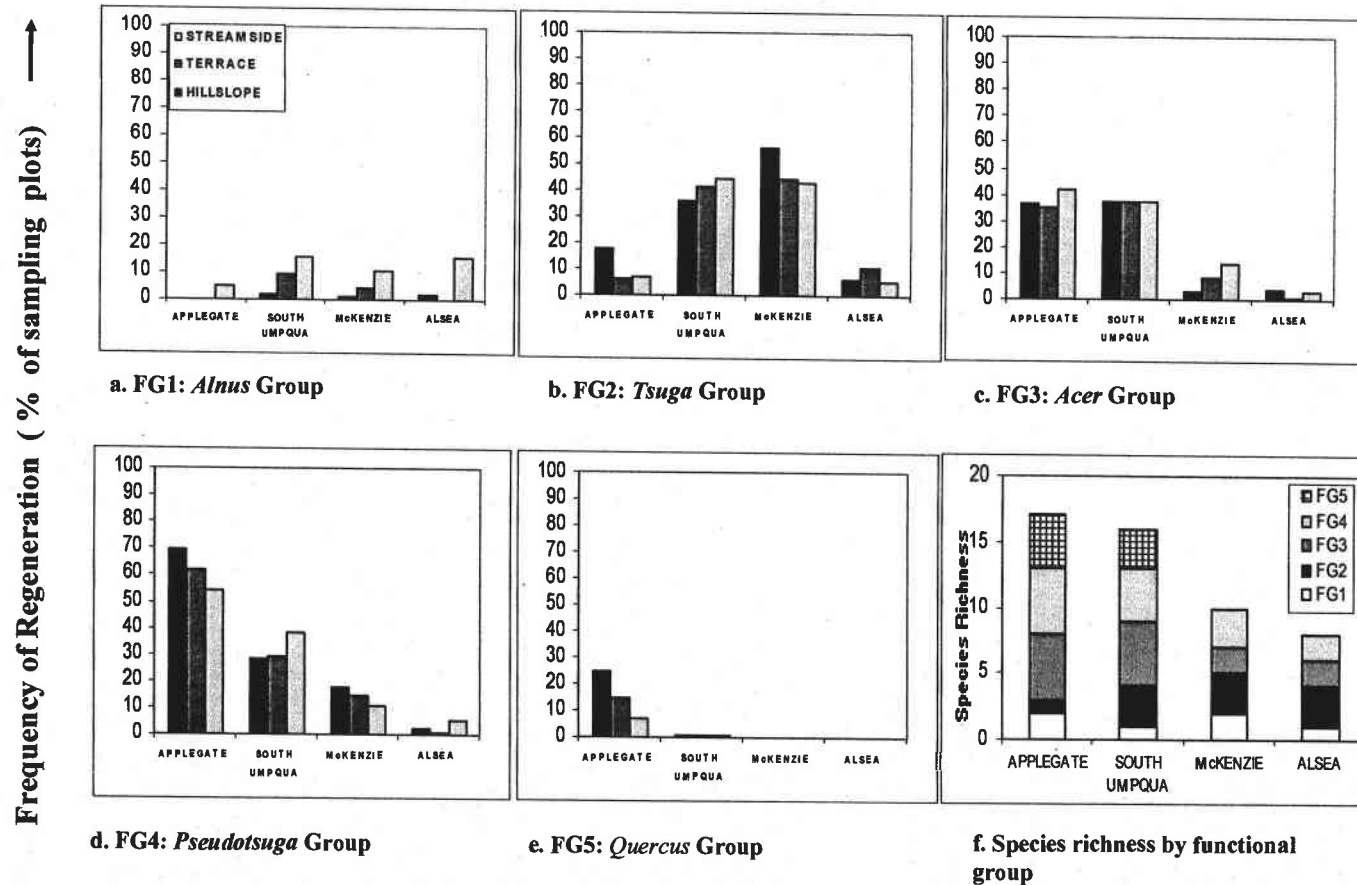


Figure 4.5 a-f. (a-e.) Bar graphs portraying frequency (%) of sampling plots with tree regeneration for each functional group in each topographic class (left to right: streamside, terrace toeslope, hillslope) in each watershed; (f) Total species richness in each study watershed, and the proportion in each of the functional groups.

Table 4.3. Mean (+ standard deviation) seedlings per hectare for each species (arranged by functional group) and for all species for sampling plots in three topographic positions (streamside, terrace, hillslope) of each study watershed in the riparian inventory. Full species names are provided for each species code in Table 4.1.

			APPLEGATE			SOUTH UMPQUA		
			Streamside	Terrace	Hillslope	Streamside	Terrace	Hillslope
			Seedlings/ha (+s.d.)			Seedlings/ha (+s.d.)		
FG1	<i>Alnus</i> Group	ALRH	108.8 (335.4)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
		ALRU	9.3 (37.3)	0.0 (0.0)	0.0 (0.0)	142.3 (164.9)	369.3 (1096.9)	5.7 (15.7)
		POTR	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
FG2	<i>Tsuga</i> Group	PISI	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
		TABR	28.0 (51.3)	25.2 (42.2)	115.5 (152.8)	40.7 (47.6)	152.9 (288.4)	63.1 (127.4)
		THPL	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	23.2 (56.3)	31.7 (72.9)	28.7 (62.4)
		TSHE	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	966.9 (1477.4)	744.4 (1298.9)	1092.4 (2331.6)
FG3	<i>Acer</i> Group	ABGR	12.4 (22.2)	25.2 (48.8)	15.6 (37.1)	148.1 (205.8)	199.1 (266.9)	186.4 (186.9)
		ACGL	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	2.9 (11.6)	23.1 (92.3)	0.0 (0.0)
		ACMA	391.6 (787.0)	267.8 (332.8)	90.5 (100.8)	363.0 (1001.3)	291.4 (982.3)	120.4 (373.8)
		CHLA	9.3 (37.3)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
		CONU	3.1 (12.4)	6.3 (16.1)	25.0 (41.9)	8.7 (25.3)	5.8 (15.8)	11.5 (26.5)
		FRLA	118.1 (371.1)	28.4 (94.5)	103.0 (350.7)	0.0 (0.0)	0.0 (0.0)	2.9 (11.5)
		CACH	18.6 (40.1)	63.0 (108.4)	53.1 (94.4)	31.9 (62.8)	40.4 (84.1)	45.9 (99.1)
FG4	<i>Pseudotsuga</i> Group	CADE	37.3 (89.9)	15.8 (28.4)	59.3 (94.0)	14.5 (47.1)	103.9 (403.4)	17.2 (57.7)
		PILA	9.3 (27.0)	9.5 (19.0)	18.7 (48.0)	0.0 (0.0)	0.0 (0.0)	2.9 (11.5)
		PSME	136.7 (155.7)	211.1 (270.6)	265.4 (316.9)	235.2 (200.3)	181.8 (258.7)	83.1 (102.2)
		QUCH	363.6 (626.2)	557.6 (697.5)	749.3 (974.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
		ARME	15.5 (39.4)	0.0 (23.6)	71.8 (268.7)	2.9 (11.6)	0.0 (0.0)	0.0 (0.0)
FG5	<i>Quercus</i> Group	PIJE	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	2.9 (11.5)	2.9 (11.5)
		PIPO	0.0 (0.0)	0.0 (23.6)	9.4 (35.1)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
		QUGA	0.0 (0.0)	37.8 (70.1)	115.5 (224.8)	11.6 (46.5)	0.0 (0.0)	0.0 (0.0)
		QUKE	12.4 (28.7)	37.8 (81.8)	106.2 (222.6)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)

Table 4.3 (Continued).

			<u>McKENZIE</u>			<u>ALSEA</u>		
			<u>Streamside</u>	<u>Terrace</u>	<u>Hillslope</u>	<u>Streamside</u>	<u>Terrace</u>	<u>Hillslope</u>
			Seedlings/ha (+s.d.)			Seedlings/ha (+s.d.)		
FG1	<i>Alnus</i> Group	ALRH	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
		ALRU	163.5 (556.1)	11.5 (35.6)	8.7 (34.7)	11227.2 (34441.2)	0.0 (0.0)	273.0 (1079.9)
		POTR	8.8 (25.4)	43.1 (172.3)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
FG2	<i>Tsuga</i> Group	PISI	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	17.3 (58.1)	0.0 (0.0)	0.0 (0.0)
		TABR	35.0 (60.3)	40.2 (64.7)	190.8 (619.8)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
		THPL	148.9 (230.2)	316.0 (1072.3)	101.2 (146.5)	5.8 (15.8)	5.7 (15.6)	2.8 (11.4)
		TSHE	750.3 (1121.6)	1780.9 (3731.2)	974.1 (1149.7)	118.3 (405.3)	102.6 (272.2)	190.5 (521.2)
FG3	<i>Acer</i> Group	ABGR	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
		ACGL	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
		ACMA	192.7 (648.5)	31.6 (81.7)	8.7 (18.6)	5.8 (15.8)	2.8 (11.4)	11.4 (20.3)
		CHLA	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
		CONU	40.9 (151.5)	2.9 (11.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
		FRLA	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	11.5 (46.2)	0.0 (0.0)	0.0 (0.0)
		CACH	8.8 (25.4)	63.2 (153.7)	75.2 (180.2)	0.0 (0.0)	2.8 (11.4)	2.8 (11.4)
FG4	<i>Pseudotsuga</i> Group	CADE	5.8 (16.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
		PILA	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
		PSME	40.9 (68.0)	43.1 (95.6)	40.5 (95.3)	43.3 (83.4)	0.0 (0.0)	48.3 (193.4)
		QUCH	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
		ARME	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
FG5	<i>Quercus</i> Group	PIJE	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
		PIPO	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
		QUGA	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
		QUKE	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)

Regeneration of FG5 (*Quercus* Group) was limited to the Applegate and South Umpqua watersheds and typically occurred at higher topographic positions (Figure 4.5e, Table 4.3). No species were abundant. *Quercus kelloggii* Newberry was the most common, followed by *Quercus garryana* Dougl. and *Arbutus menziesii* Pursh. *Pinus ponderosa* Dougl. and *Pinus jeffreyi* Grev. & Balf. were uncommon and occurred primarily at high microelevations.

Environmental Factors Associated with Regeneration

For FG1 (*Alnus* Group), CART analysis identified fluvial scouring as the first and most important factor splitting sites with low and high levels of regeneration (Proportional Reduction in Error (PRE) = 0.31, Figure 4.6a). When SCOUR was excluded from analysis, height above stream became the primary splitting variable, with highest regeneration at less than ~ 1.2 m above the stream edge. However, SCOUR reduced error an additional 5%, suggesting that evidence of actual flood disturbance was important for this group. At sites with high scour, low litter depth (LDEPTH) (< 2.5 cm) distinguished plots with the most abundant regeneration (PRE = 0.08). Total PRE for the FG1 CART model was 0.39.

Variation in Growing Degree Days (GDDTOT) formed the first division in the regression tree for FG2 (*Tsuga* Group) (PRE = 0.22, Figure 4.6b). Seedlings of this group were most common in the relatively cool sites of the Cascades watersheds. While it is clear that most of the species in FG2 are entirely missing from the warm, dry Applegate watershed, it is not clear whether the low regeneration of these species in the cool, moist Alsea watershed is driven by climate or other confounding factors (e.g. shrub competition, fire history) (see Wimberly and Spies 2001). At plots with low GDDTOT (< 3864 yr⁻¹), areas with moderate volumes of large woody debris present (LWDVOL > 181.3 m³/ha) had nearly ten times the regeneration densities as sites with less wood (212.8 s/ha vs. 17.7 s/ha,

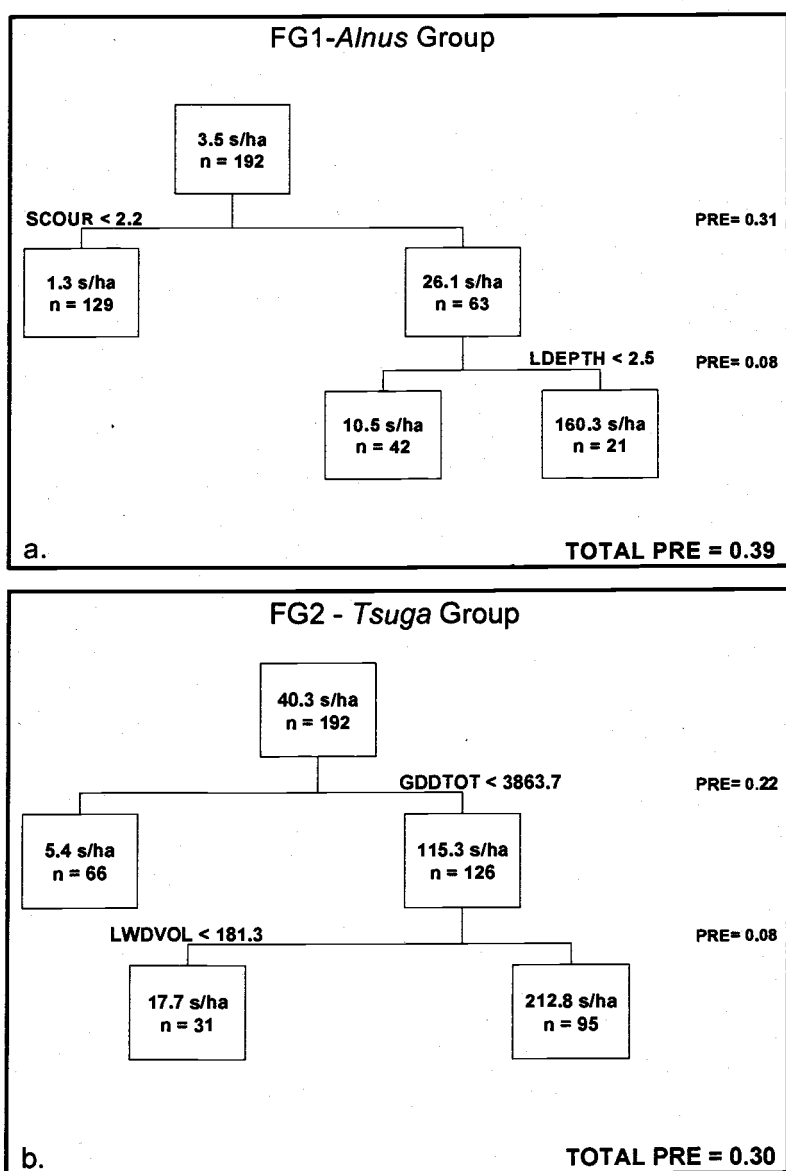


Figure 4.6 a-e. Regression tree diagrams from CART analysis for each functional group. Each split is labeled with the discriminating variable and the splitting value. Placement of the variable indicates relationship: if the variable is over left leg of split, the variable is positively associated with seedling abundance; if variable is over right leg, the relationship is negative. Boxes at each terminal node contain median seedling densities/hectare and the number of samples meeting the splitting criteria for that node. See table 4.2 for variable list.

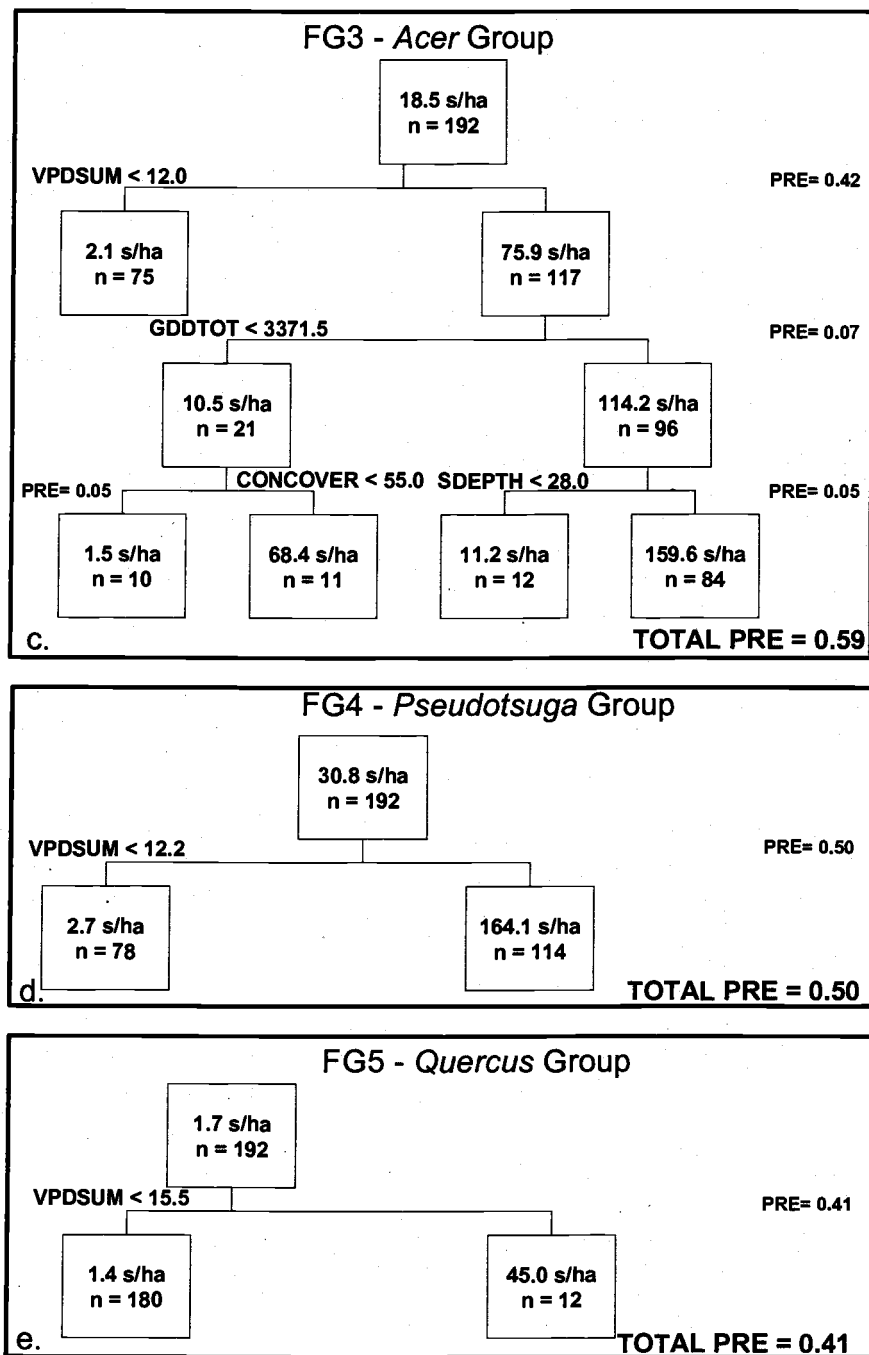


Figure 4.6 (cont.)

respectively) (PRE = 0.08, Figure 4.6b). The importance of large wood for tree establishment was strongly influenced by *T. heterophylla*, for which over 80% of all seedlings occurred on downed logs. Overall PRE for the FG2 CART model was relatively low at 0.30.

For FG3 (*Acer* Group), variation in summer vapor pressure deficit (VPDSUM) as the primary factor distinguishing sites with high and low regeneration (PRE = 0.42, Figure 4.6c). Seedlings of this group were rare in wet coastal sites with low VPDSUM (< 12.0 millibars). At drier noncoastal sites, GDDTOT was the next factor splitting regeneration patterns (PRE = 0.07). Within sites with low growing season temperatures (i.e., the McKenzie watershed), seedlings were most abundant at sites with low proportions of conifer cover (< 55 %) in the canopy (PRE = 0.05). At warmer sites in southwest Oregon, seedlings were found on deeper soils (SDEPTH > 28.0 cm). Total PRE for the FG3 CART model was 0.59.

For FG4 (*Pseudotsuga* Group), summer vapor pressure deficit was the only factor selected by CART for distinguishing sites with high and low regeneration (PRE = 0.50, Figure 4.6d). Regeneration levels in the drier climates of southwest Oregon were much higher than in wetter climates with lower vapor pressure deficits (median regeneration levels of 164.1 and 2.7 seedlings/ha, respectively, Figure 4.6d).

The driest climates of the Applegate and South Umpqua watersheds (VPDSUM > 15.5 mb) had much higher abundances of FG5 (*Quercus* Group) seedlings than all the other sites (Figure 4.5e). VPDSUM was the only splitting variable selected (PRE = 0.41, Figure 4.5e).

Nurse Logs

Of the 23 tree species, 12 (55%) occurred on downed logs. Nurse logs were an important regeneration surface for conifers (50.2% on logs), but were much less

important for hardwoods (3.7% on logs). The proportion of total seedlings on logs differed strongly among conifer species, from >75% for *P. sitchensis* and *T. heterophylla*, 20-35% for *T. plicata*, *T. brevifolia*, and *P. menziesii*, to 0% for *Pinus* spp. Among hardwood species, the proportions on logs were much lower, with a high of 11 % for *C. chrysophylla* and less than 2% for all other species. The proportion of total conifer regeneration on nurse logs increased sharply from south to north (Figure 4.7).

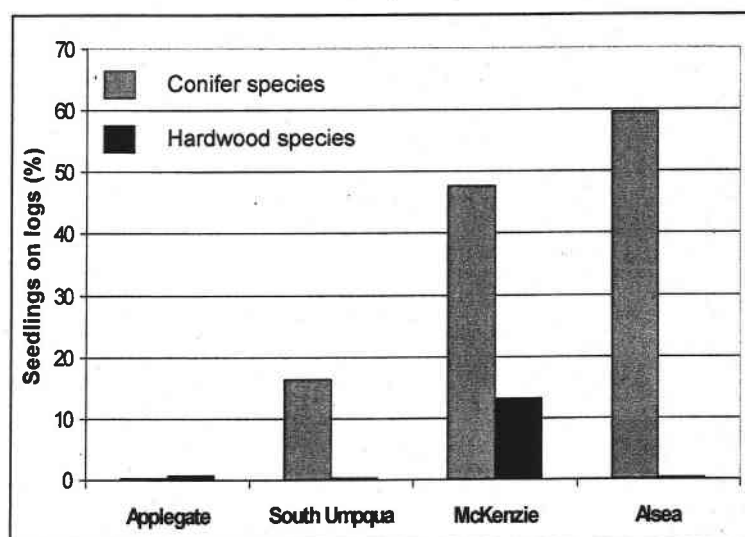


Figure 4.7. Percentages of seedling found on nurse logs for hardwood and conifers seedlings in each study watershed with all species weighted equally.

Gap-Forest Comparisons

Gaps had a greater abundance and diversity of regenerating trees than forest plots in all four watersheds, especially for FG1 (*Alnus* Group), which had 2 to 10 fold higher seedling densities in gaps than in adjacent forest sites (Table 4.4). In the Alsea watershed, *A. rubra* seedlings were over 100 times as abundant in gap environments as in forested areas. Species in FG3-5 (*Acer*, *Pseudotsuga*, and

Quercus Groups) responded similarly to gaps, typically with much higher seedling abundances in gaps than in the adjacent forest, along with a general decline in abundance in both settings from south to north (Table 4.4). *A. macrophyllum* was the only FG3 (*Acer* Group) species that regenerated in the Alsea watershed. *F. latifolia* was the only species in FG3 that occurred in greater abundances in forest interiors than gaps (31 vs. 25 seedlings total). FG4 (*Pseudotsuga* Group) showed similar regeneration patterns to FG3 (*Acer* Group), except all species were equal to or more common in gaps than forests, and abundances declined even more sharply from south to north (Table 4.4). Seedlings of this group were very rare in forest interiors of the McKenzie or Alsea watersheds. *P. menziesii* was the only member of this group to regenerate in the Alsea watershed and only in gaps there (Table 4.4).

In the gap-forest dataset, species in FG5 (*Quercus* Group) only occurred in the Applegate watershed, where all species were more common in gaps (Table 4.4). *A. menziesii* and *Q. kelloggii* were the most common species, but absolute seedling numbers were low (Table 4.4). Only the two oak species were encountered in forest settings (Table 4.4); these were dry, open *Quercus-Pinus-Pseudotsuga* woodlands.

FG2 (*Tsuga* Group) was the only group that showed generally higher levels of regeneration under a forest canopy (Table 4.4). *T. heterophylla* was more abundant in forest interiors in two of the three watersheds where it was recorded. *T. brevifolia* was more common in forests than gaps in all three watersheds where it was encountered (Table 4.4). *T. plicata* was more common in forests than in gaps in the South Umpqua watershed (5 vs. 2 seedlings, Table 4.4) but more abundant in gaps than forests in the McKenzie watershed (47 vs. 12 seedlings, Table 4.4). *T. plicata* seedlings in the McKenzie often occurred on disturbed streamside gaps with mineral soils. *T. plicata* seedlings were not encountered in gaps or forest sites of the Alsea or Applegate watersheds.

Table 4.4. Seedlings per hectare for each species are for sixty pooled gap and forest samples in each watershed. Full species names are provided for each species code in Table 4.1.

		APPLEGATE	SOUTH UMPQUA		McKENZIE		ALSEA			
		(Seedlings/ha)								
	Functional Group	Species Code	Gaps	Forest	Gaps	Forest	Gaps	Forest	Gaps	Forest
FG1	Alnus Group	ALRH	4.6	0.0	116.1	0.0	0.0	0.0	0.0	0.0
		ALRU	0.0	0.0	200.9	132.3	302.9	13.2	8529.0	74.7
		POTR	0.0	0.0	0.0	0.0	116.8	66.2	0.0	0.0
FG2	Tsuga Group	PISI	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		TABR	27.7	372.8	147.3	155.2	64.9	494.4	0.0	0.0
		THPL	0.0	0.0	8.9	22.8	203.4	53.0	0.0	0.0
		TSHE	0.0	0.0	772.3	1277.7	990.9	1509.7	34.5	13.2
FG3	Acer Group	ABGR	189.6	36.4	799.1	219.0	4.3	0.0	0.0	0.0
		ACGL	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		ACMA	2223.8	309.2	1000.0	684.5	445.7	35.3	51.8	13.2
		CHLA	32.4	13.6	0.0	0.0	0.0	0.0	0.0	0.0
		CONU	9.2	4.5	102.7	9.1	4.3	0.0	0.0	0.0
		FRLA	115.6	141.0	17.9	0.0	0.0	0.0	25.9	17.6
FG4	Pseudotsuga Group	CACH	180.3	18.2	62.5	41.1	51.9	8.8	0.0	0.0
		CADE	120.2	22.7	22.3	9.1	8.7	0.0	0.0	0.0
		PILA	32.4	0.0	4.5	4.6	0.0	0.0	0.0	0.0
		PSME	906.2	150.0	879.4	223.6	125.5	8.8	99.2	0.0
FG5	Quercus Group	QUCH	739.7	291.0	0.0	0.0	0.0	0.0	0.0	0.0
		ARME	78.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		PIJE	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		PIPO	13.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		QUGA	37.0	18.2	0.0	0.0	0.0	0.0	0.0	0.0
		QUKE	106.3	31.8	0.0	0.0	0.0	0.0	0.0	0.0
TOTAL			4817.4	1409.5	4133.8	2779.1	2319.3	2189.5	8740.4	118.7

Evaluation of the Regeneration Model

The life history / context regeneration model correctly predicted differences in regeneration in 79.7% of the gap/forest and inter-watershed comparisons for all functional groups (Table 4.5). For all groups except FG3 (*Acer* Group), accuracy exceeded 75% and within group comparisons were all significant at the $P < 0.05$ level (X^2 Test). For FG3, accuracy was 61.1 % and nonsignificant. For FG3, our model predicted that gap environments of southwest Oregon would be too severe for effective regeneration. In reality, the highest regeneration levels occurred in these settings. With regard to gaps, FG3 showed very similar patterns to FG4. If the predictions for FG4 (*Pseudotsuga* Group) were applied to FG3, accuracy would improve to 77.8% and become significant. With this shift, accuracy of the regeneration model would rise to 83.5% overall.

Table 4.5. Percent accuracy and statistical significance for predictions of the regeneration model (Figure 4.2) for gap inventory dataset. The table lists accuracy for each functional group, all functional groups combined, and when predictions for FG4 are applied to FG3.

Group	Correct Predictions	Total Comparisons	Accuracy (%)	Probability (X^2 Test)
FG1 <i>Alnus</i> Group	14	18	77.8	P= 0.018
FG2 <i>Tsuga</i> Group	15	18	83.3	P= 0.005
FG3 <i>Acer</i> Group	11	18	61.1	P= 0.346
FG4 <i>Pseudotsuga</i> Group	16	18	88.9	P= 0.001
FG5 <i>Quercus</i> Group	7	7	100.0	P< 0.05
ALL GROUPS	63	79	79.7	P< 0.0001
FG3 SHIFTED TO FG4	14	18	77.8	P= 0.018
OVERALL ACCURACY				
WITH FG 3 SHIFTED	66	79	83.5	P< 0.0001

DISCUSSION

Despite a diversity of species and regeneration environments, riparian tree regeneration in western Oregon showed predictable patterns. Four of our five functional groups showed strong geographic scale patterns in regeneration consistent with their reported environmental tolerances. Less shade tolerant species were all more abundant in gaps and drought tolerant species were all more common in southwest Oregon. To our surprise, however, riparian forests in the relatively harsh climates of southwest Oregon had not only a rich riparian tree flora, but the higher frequency of tree regeneration than forests in northwest Oregon..

Why should the frequency and abundance of most species decline in wetter climates? In the wet northern watersheds, denser vegetation, and the presence of clonal shrub competitors may affect the frequency and diversity of tree regeneration. *Rubus spectabilis* Pursh, a clonal shrub that increased sharply in importance along the dry to wet climate gradient, may have been one climate-associated factor shaping the regeneration environment. We seldom saw seedlings of any species under dense *R. spectabilis* shrubfields, a pattern noted by others in the Oregon Coast Range (Tappeiner et al. 1991, Minore and Weatherly 1994, Pabst and Spies 1999, Hibbs and Bower 2001). Overall regeneration frequencies were lowest on terraces of the Alsea watershed (Figure 4.5, Table 4.3), sites with the highest mean *R. spectabilis* cover (40.6%). From this regional minimum, tree regeneration increased toward relatively more disturbed streamsides (primarily by *A. rubra*) and towards drier hillslopes or climate regions, where *R. spectabilis* was less abundant or absent.

The cooler, somewhat drier riparian forests of the McKenzie watershed, where *T. heterophylla* often cast deep shade on floodplains, appeared to form a secondary minimum for establishment of many tree species. Even species of reportedly high shade tolerance (e.g., *A. grandis*, *Cornus nuttallii* Aud.) regenerated only in gaps in the dense *T. heterophylla*-dominated forests (Table 4.4). These

same sites had abundant *T. heterophylla* regeneration under the forest canopy (Table 4.3), suggesting that through shading and possibly litter accumulation, *T. heterophylla* modifies sites to its own advantage, as has been suggested for *T. canadensis* in eastern North America (Collins 1990).

FG1 (*Alnus* Group) regeneration showed a stronger relationship to local than regional controls. Trees in this group occurred most frequently on moist, well-lit mineral substrates near streamsides in all watersheds (Figure 4.5a) and were always more abundant in gaps than forests (Table 4.4). Despite these clear regeneration requirements for the group, our finding of a dramatic increase in the densities of *A. rubra* seedlings in gaps of the wet Alsea watershed when compared to gaps in the drier watersheds (Table 4.4), suggests climate affects disturbance response for that species. Regeneration of *A. rubra* was closely linked to streamsides in the drier watersheds, but the species readily colonized disturbance gaps on hillsides in the wettest climates.

Effects of context (climatic setting) on disturbance association were also evident for a number many other species. Moderately shade tolerant species, such as *P. menziesii* and *C. decurrens*, regenerated under the relatively open forest canopies in the driest climates where *R. spectabilis* and *T. heterophylla* were absent. In the presence of these species, regeneration was more closely tied to gaps. Veblen (1989) described a very similar pattern for the canopy emergent *Nothofagus dombeyi* along a climate gradient spanning the southern Andes. At cold, high elevation sites, or dry sites east of the Andes crest, where clonal bamboos or more shade tolerant trees were absent, *N. dombeyi* readily regenerated in forest gaps (Veblen 1989). In contrast, in the very wet forests of the western Andes, where these two competitors were present, *N. dombeyi* regenerated primarily in large open areas. Veblen's (1989) example and our data support a general conclusion: the majority of tree species do not employ a fixed regeneration mode (*sensu* Veblen 1992) or strategy (Grime 1977, Whitmore 1989), but reproduce opportunistically wherever local conditions are suitable.

Our study confirmed that nurse logs are important regeneration sites for conifers in wet riparian forests, but suggested they are less important in drier forests (Figure 4.6). This may be due to changes in nurse log moisture, competitive influence, or species composition. Our data did not allow us to distinguish these factors. Nurse logs were used most frequently by *T. heterophylla* and *P. sitchensis*, as noted by others in the region (Harmon and Franklin 1989, Pabst and Spies 1999). We also noted moderate use of nurse logs by the conifers *P. menziesii*, *T. plicata*, *T. brevifolia*, and the evergreen hardwood *C. chrysophylla*. However, pines and most hardwoods rarely occurred on logs.

Disturbance gaps yielded greater tree diversity and higher levels of regeneration for most species than the forest interior, suggesting gap-dynamics are important in these riparian forests, as elsewhere (Hibbs 1982, Pickett and White 1985, Veblen 1989, Whitmore 1989). *T. brevifolia* was the only species that consistently regenerated at higher levels in forest interiors. The results for this species and for *T. heterophylla*, however, suggest that some riparian tree species do benefit from a protective forest canopy during establishment.

Our life history-context model proved useful for predicting regeneration success of our functional groups across the climatic and disturbance gradients studied. Although it apparently overestimated the negative effects of gap microclimate for drought and heat sensitive species in southwest Oregon, it accurately predicted the general decline in abundance of less shade tolerant functional groups and their closer association with gap environments in northwest Oregon.

The field data from this study support a revised, simplified regeneration model that combines FG3 (*Acer* Group) and FG4 (*Pseudotsuga* Group), leading to only four regeneration domains across the range of environments studied. Although published data suggested important differences between species in the two groups, these differences may be relatively less than previously described. The striking declines in regeneration of both groups south to north suggest that they show

similar regeneration responses across the range of environmental conditions we studied.

The patterns in seedling abundances we observed tell only a partial story of regenerative processes in these forests. Developmental changes in shade tolerance, growth rates, or other factors that affect tree survival at later life stages were not studied. Moreover, the current dominance of *P. menziesii* in mature riparian forests of northwest Oregon cannot be explained by the fine-scale disturbances we recorded. Regeneration of that species was infrequent in gaps and nearly absent in forest interiors. Nierenberg and Hibbs (2000) also speculated that there may be insufficient disturbance to maintain riparian tree cover in the Oregon Coast Range, where *R. spectabilis* maintains long-term dominance. Given the longevity of *P. menziesii*, periodic large-scale disturbances (e.g., fire, large floods) likely played a critical role in establishing its current dominance in many riparian forests of northwest Oregon (Wimberly and Spies 2001). As Sakai et al. (1999) demonstrated, information on infrequent, catastrophic floods as well as finer scale effects of smaller floods and gap processes were both necessary to explain the current structure of a *Quercus-Ulmus* riparian forest in Japan. Studies spanning a larger spectrum of disturbance types, sizes, and intensities may be needed to fully understand the regenerative dynamics of these riparian forests.

We conclude that in geographically complex regions, such as western Oregon, multiscale factors create diversity in regeneration environments, and correspondingly varied riparian regeneration dynamics. We noted a marked geographic shift in the frequency and abundance of tree regeneration and the use of riparian nurse logs across the climate gradient from southwest to northwest Oregon. Our life history/context regeneration model, which linked species drought and shade tolerance with environmental changes caused by climate and disturbance, successfully predicted regeneration patterns of most species. These findings illustrate the value of integrating insights from life history, environmental gradients, and disturbance to understand natural regenerative processes in riparian forests.

CHAPTER FIVE - SUMMARY, MANAGEMENT IMPLICATIONS, AND CONCLUSIONS

The objective of this dissertation was to explore the effects of local and regional controls on woody vegetation in western Oregon riparian forests. I noted pronounced shifts in riparian forest composition, diversity, and tree regeneration patterns across the climate gradient from dry southwest to wet northwest Oregon. In this final chapter, I summarize key findings from the three field studies, and I discuss the implications of these studies for riparian forest conservation, management, and restoration in western Oregon.

CONTROLS ON WOODY PLANT DISTRIBUTION

Despite considerable spatial and temporal variation, there appear to be relatively predictable climate-driven changes in riparian forest structure and composition across western Oregon. The observation that climatic moisture (indexed by vapor pressure deficit in summer) was the primary correlate of species compositional change is consistent with regional studies of upland forests (Zobel et al. 1976, Ohmann and Spies 1998), and demonstrated that the majority of riparian species respond to regional climate variation, or perhaps more accurately, to changes in local competitive pressures across the gradient.

I noted evidence that climate can directly govern the species present in riparian forests, but more species appeared to be affected by changes in biotic and abiotic conditions (i.e., competition, understory light availability) that changed across the gradient. Across the study area, these direct and indirect controls on species distributions appeared to create three geographic boundaries with noticeable changes in the riparian flora. The first, apparently a direct climatic boundary, occurred at the edge of the fog belt approximately 10 km from the Pacific Ocean, marking the landward extent of *Picea sitchensis*, *Vaccinium ovatum*, and *Menziesia ferruginea*. The

distinctiveness of the *Picea sitchensis* zone has been described by Franklin and Dyrness (1988), and its importance for riparian vegetation was suggested by Wimberly and Spies (2001). The second direct climatic boundary appeared to run east/west along the Rogue / Umpqua divide and southward along the eastern shoulder of Grayback Mountain in southwest Oregon. A number of mesophytic species with wide distributions in western Oregon, including *Tsuga heterophylla* (Raf.) Sarg., *Thuja plicata* Donn, *Acer circinatum* Pursh, and *Ribes bracteosum* Dougl., were present in the South Umpqua watershed but were either absent in the Applegate watershed or were confined to the relatively mesic western edge of the watershed. This finding is consistent with the prior designation of the eastern Siskiyou Mountains as a distinct environmental and floristic region, marked by the notable absence of many mesophytic species (Waring 1969).

Despite evidence of direct climatic thresholds for some species, the majority of species we encountered occurred more frequently in the comparatively harsh climates of southwest Oregon. The Applegate watershed supported a rich southern flora, supporting assertions that the upper Rogue region acts as a northern extension of the California Floristic Province (Howell 1957, Stebbins and Major 1965, Hickman 1993). The finding that more species occur in southwest than northwest Oregon suggest that the effect of climate on the majority of species is indirect, expressed through its influence on stand density and the presence, vigor, and topographic amplitude of strong competitors, such as *Rubus spectabilis* Pursh. For example, *R. spectabilis* was abundant in all topographic positions in the Alsea watershed, limited to wet floodplains and streamsides in the McKenzie watershed, a rare wetland obligate in the South Umpqua watershed, and lacking entirely from the Applegate watershed. In dense forests of northwest Oregon, where *R. spectabilis* dominates the understory, many southern species were either absent or occurred infrequently.

We noted three major floristic elements across the climate gradient, a xerophytic flora centered in southwest Oregon, as noted above, a somewhat less species-rich and more shade-tolerant flora in the Cascades, and a unique but

comparatively species-poor coastal flora. Whereas direct climatic limitations (i.e., vapor pressure deficits, drought) appeared to cause some impoverishment of mesophytic species from north to south across the gradient, indirect climatic effects (i.e., increased shrub competition, lower light) appeared to filter the southern flora in the opposite direction. There appeared to be a gradual loss of the species-rich southern flora from the Applegate to the South Umpqua and the eastern McKenzie watersheds, with its replacement by the Cascades flora. Forests in these three areas were roughly comparable in diversity, but varied in composition. An abrupt loss of the southern flora and an impoverishment of the Cascades flora occurred in the maritime climates and *R. spectabilis* dominated riparian forests of the western McKenzie and Alsea watersheds. This transition zone occurred some kilometers inland from the coastal fog zone and may represent a third, riparian specific, biogeographic boundary, marked by a sharp increase in *R. spectabilis* vigor and topographic amplitude, effectively excluding many southern species.

Riparian gradient structure also changed markedly across the climate gradient from dry southwest to wet northwest Oregon. Moisture gradients from streamsides to hillslopes decreased, total cover increased, and understory light decreased across the gradient.

However, I learned that local heterogeneity in regional riparian forests is surprisingly complex, with many factors affecting local species distributions. Although moisture heterogeneity was greatest in southwest Oregon, as expected, the contrast in vegetation composition from the relatively open, drier forests there to adjacent disturbed streamsides areas was no more pronounced than in wetter riparian forests of the Cascades, where dark forests and bright disturbed area were also floristically distinct. The presence of rocky outcrop areas in riparian forests also appeared to add another important form of heterogeneity, and some species occurred preferentially at such sites (*Ribes roezlii* Regel, *Polystichum imbricans* (D. Eaton) D. H. Wagner). The presence of *R. spectabilis* also appeared to be associated with low heterogeneity, suggesting patterns of dominance may partially control heterogeneity

and beta diversity. Of all the phenomena I observed, I believe riparian heterogeneity may present the richest area for future study.

Local disturbances appeared to have less influence than climate or topography, for most species, but several species showed strong associations with the presence of gap disturbance (*Rubus leucodermis* Dougl., *Rubus parviflorus* Nutt., *Ribes sanguineum* Pursh). Several other species appeared to be specifically associated with the mineral soils and high light levels provided by fluvial disturbance (*Populus trichocarpa* T. & G., *Salix sitchensis* Swanson, *Alnus* spp.). Yet other species (e.g., *Taxus brevifolia* Nutt. and the fern *Polystichum munitum* (Kaulf.) Presl.) were strongly associated with undisturbed forest interiors.

In general, I learned that riparian forest vegetation in western Oregon shows strong regionalization and close linkages with the flora of the surrounding landscape. Topographic gradients from streamside to hillslope and disturbances of fluvial or terrestrial origin also appear to be important for a number of woody plant species. Together, these factors create a complex of gradient and mosaic phenomena that govern distributions at multiple scales.

CONTROLS ON WOODY PLANT DIVERSITY

As with species distributions, plant diversity in riparian forests appears to be an outcome of many interacting factors. In the multiscale analysis of woody plant diversity in riparian forests, I recorded evidence for an indirect model of climatic control on richness. In support of this model, understory light and moisture heterogeneity decreased from the driest to the wettest climates, coincident with declines in alpha, beta, and hectare scale diversity. Climatic favorability, as indexed by GPP, showed strong negative relationships with tree, shrub, and total woody plant richness that explained the majority of the variation in stepwise multiple regression models. Local gap disturbances yielded slightly higher richness at most sites, but the magnitude of this effect was not a direct function of GPP.

Although climate probably plays a more important role in structuring the riparian environment than is often thought, it is by no means the only important factor. In addition to the effects of the climate gradient, I also saw evidence of local and watershed influences on both alpha and beta diversity in these forests. Fluvial disturbance, in particular, appeared to be an important control on alpha diversity near streamsides. This study points toward an integrated conceptual model whereby landscape scale controls such as climate and watershed position complement and interact with local controls (i.e. vegetation structure, environmental gradients) to jointly govern riparian plant diversity across scales and topographic positions.

Within the framework of this conceptual model, I propose that effects of climate will be most important in explaining patterns of diversity in low order, nonalluvial streams and that occur in forested landscapes or span steep climatic gradients. Given the extent of such mountain streams in the western U.S. and worldwide, the findings reported in this dissertation have broad relevance. Along larger alluvial streams or rivers, where channel migration is more pronounced and periods of flooding are sustained for longer periods, local hydrologic patterns may play the dominant role in shaping vegetation diversity, as has been noted elsewhere (Nilsson et al. 1989). The relative importance of landscape scale and local controls on riparian plant diversity, therefore, is likely fluid, depending upon the landscape setting and stream type.

CONTROLS ON RIPARIAN TREE REGENERATION

Life history attributes of riparian tree species and hypothesized regional shifts in abiotic and competitive pressures provided a powerful conceptual model for predicting tree regeneration at both local and regional scales. A functional classification of riparian trees based on published life history attributes yielded five

groups distinguished primarily by shade and drought tolerance: FG1 – *Alnus* Group (drought and shade intolerant); FG2 – *Tsuga* Group (drought intolerant, very shade tolerant); FG3 – *Acer* Group (moderately drought tolerant, shade tolerant); FG4 – *Pseudotsuga* Group (drought tolerant, moderately shade tolerant); and FG5 – *Quercus* Group (very drought tolerant, shade intolerant). Four of the five functional groups showed strong local regional scale patterns in regeneration consistent with their reported environmental tolerances.

For most species, the climate gradient appeared to exert its greatest effect not through direct abiotic controls on seedlings, but through its effects on the competitive environment. Despite greater drought stress, southwest Oregon had the richest riparian tree flora and highest frequency of tree regeneration. In the northern watersheds, dense forest canopies and the presence of clonal shrub competitors were likely both important in explaining the lower frequency and diversity of tree regeneration. A strong and predictable south to north decrease in regeneration for most of the less shade tolerant tree species illustrated the importance of shade tolerance for predicting regeneration success in riparian forests of northwestern Oregon. *A. rubra* was the primary exception to the south to north regional decline in less shade tolerant species. Although *A. rubra* regenerated primarily on disturbed streamsides, the dramatic increase in abundance in the Alsea watershed suggested that the wetter climate there greatly increases the range of habitats where that drought sensitive species can establish. However, the finding that highest and lowest regeneration densities for the whole study occurred on disturbed streamsides and adjacent *R. spectabilis* dominated terraces in the Alsea watershed, provided stark testimony to the effectiveness of local competitive controls on tree regeneration.

Whereas controls on seedling establishment were primarily local for FG1, and to a lesser degree for *T. heterophylla* in FG2, regional scale gradients were important for many species. Less shade tolerant tree species regenerated most abundantly and frequently in southwest Oregon and declined sharply in the wetter forests of northwest Oregon where *R. spectabilis* and *T. heterophylla* were often

strongly dominant. A model linking life history characteristics and climate-driven changes in microclimate and understory light predicted most of these contextual shifts and proved valuable for interpreting spatial patterns of tree regeneration in forest interiors and disturbed environments across the climate gradient.

FOREST MANAGEMENT IMPLICATIONS

The field studies described in this dissertation highlight the breadth of species and habitats in Oregon riparian forests. Major shifts in woody plant composition, diversity, and tree regeneration frequency across the gradient from southwest to northwest Oregon, and differences in vegetation responses to disturbance require that managers pay close attention to the ecological conditions and species combinations when implementing forest management activities.

For example, the roles of drought and competition are likely to be first considerations for the survival of riparian vegetation. Along the fog-prone coastal strip, moisture stress is much less of a problem than in the interior or farther south. However, the long, moist growing season allows clonal shrubs to grow vigorously throughout the riparian corridor and to create a highly competitive environment for other woody plants. These same moist conditions make nurse logs a more favorable substrate for regeneration and a majority of conifer seedlings are found on logs in wet climates. Large logs raise the seedling relatively higher off the ground and may provide a better chance of escaping shrub competition during establishment and early growth (Harmon and Franklin 1989, Minore and Weatherly 1994). Where clonal shrubs are well established and wood debris is absent, small scale disturbances, such as treefall gaps, may have little effect on woody plant diversity or tree regeneration on the ground. Any opportunities for tree establishment will be relatively ephemeral unless the disturbance is large enough to remove the clonal species, or the tree species has rapid juvenile height growth (e.g., *Alnus* spp.). However, clonal shrub cover is a

natural aspect of unmanaged riparian forests in coastal Oregon (Nierenberg and Hibbs 2000), and strong shrub dominance does not, in itself, constitute a problem.

In the central and southern Cascades, the effect of seasonal drought is stronger, yielding greater zonation in the riparian corridors. Where it occurs, *R. spectabilis* typically occurs only on floodplain swales and stream margins and often is much less dense than in the Coast Range, allowing much more natural tree regeneration across the riparian corridor. Aspect differences are also more strongly expressed, so that north- and south-facing slopes may have a number of different species. For example, we frequently noted pines and other drought tolerant species on convex south slopes that typically did not occur on north slopes or concave microsites of the same stream.

In the Siskiyou Mountains, several widespread northern species (e.g., *Tsuga heterophylla*, *Thuja plicata*, *Vaccinium parvifolium*) are absent or rare, yet a larger number of southern species occur, yielding a highly diverse and distinctive riparian flora. This region is prone to severe summer drought and high surface temperatures, which are likely key considerations in managing riparian forests in this subregion. Restoration efforts should take this into account by paying close attention to aspect, height above stream, and exposure of planted tree or shrub seedlings. Timber harvest or other management activities will also likely have different effects on understory species depending upon aspect or height above the stream. Intense surface heating and large vapor pressure deficits in disturbed areas can be expected to be stressful for sensitive plant species. Management of these systems should blend methods developed in northwest Oregon with approaches used in California or east of the Cascades.

The interior forests of the Cascades and Siskiyou Mountains are typically richer in species, and moisture gradients are steeper, yielding greater challenges in matching species with local conditions. Nurse logs are very important tree establishment sites in the Cascades, but less so in the eastern Siskiyou forests. The decrease in use of nurse logs in southwest Oregon may be due to insufficient log

moisture, shifts in species present (i.e., pines rarely use nurse logs for regeneration), and lowered competition at the ground level.

Because the most important species and ecological processes change across the region, managers should take care to apply appropriate subregional approaches that consider the most important ecological controls and constraints.

CONCLUSIONS

The field studies in this dissertation demonstrated that climate gradients strongly influence physical and biological conditions in western Oregon riparian forests, and add to a body of landscape scale studies of riparian systems (Collins et al 1981, Baker 1989, Bendix 1994, Pabst and Spies 1998, 1999). These studies illustrate that riparian communities are not simply distinctive ecosystems, but are important parts of the landscape continuum (Whittaker 1956, 1960, Vankat 1982, Austin and Smith 1989), being both internally variable and coupled closely to the watersheds in which they occur (Vannote et al. 1980, Fetherston et al 1995, Montgomery 1999). Such insights provide an important complement to models interpreting Pacific Northwest riparian forest dynamics in terms of local fluvial processes (Gregory et al. 1991, Montgomery 1999, Johnson et al. 2000 Naiman et al 2000, Nakamura et al 2000).

Management of these systems can profit from such complementary perspectives. Managers need to understand the local hydrologic and other processes that maintain the integrity of riparian forests. They can also better do their jobs when they have a quantitative understanding of how riparian forests change in ecological conditions, composition, and dynamics from place to place.

BIBLIOGRAPHY

- Adams, J. M., and F.I. Woodward. 1989. Patterns of tree species richness as a test of the glacial extinction hypothesis. *Nature* 339:699-701.
- Alcaraz, F., S. Rios, C. Inocencio, and A. Robledo. 1997. Variation in the Riparian Landscape of the Segura River Basin, SE Spain. *Journal of Vegetation Science* 8:597-600.
- Arrhenius, O. 1921. Species and area. *Journal of Ecology* 9:95-99.
- Auble, G., and M. L. Scott. 1998. Fluvial disturbance patches and cottonwood recruitment along the upper Missouri River, Montana. *Wetlands* 18(4):546-556.
- Austin, M. P., and T. M. Smith. 1989. A new model for the continuum concept. *Vegetatio* 83:35-47.
- Bailey, J.D., C. Mayrsohn, P.S. Doescher, E. St. Pierre, and J. C. Tappeiner. 1998. Understory vegetation and in old and young Douglas-fir forests of western Oregon. *Forest Ecology and Management* 112:289-302.
- Baker, F. S. 1944. Mountain climates of the western United States. *Ecological Monographs* 14:225-254. 16-47.
- Baker, W. L. 1989. Macro and micro-scale influences on riparian vegetation in western Colorado. *Annals of the Society of American Geographers* 79(1): 65-78.
- Beach, E. W., and C. B. Halpern 2001. Controls on conifer regeneration in riparian forests: effects of seed source, substrate, and vegetation. *Canadian Journal of Forest Research* 31:471-482.
- Beckage, B. J.S. Clark, B. D Clinton, and .B. L. Haines. 2000. A long-term study of tree seedling recruitment in southern Appalachian forests: the effects of canopy gaps and shrub understories. *Canadian Journal of Forest Research* 30:1617-1631.
- Benda, L. E. 1988. Debris flows in the Tyee sandstone formation of the Oregon Coast Range. MS thesis, University of Washington.

- Bendix, J. 1994. Among-site variation in riparian vegetation of the Southern California Transverse Ranges. *American Midland Naturalist*. 132:136-151.
- Bisson, P. A., R. E. Bilby, M. D. Bryant, C. A. Dolloff, G. B. Greete, R. A. House, M. L. Murphy, K. V. Koski, and J. R. Sedell. 1987. Large woody debris in forested streams in the Pacific Northwest: past, present, and future. Pages 143-190 in E. O. Salo, and T. W. Cundy, editors. *Streamside management: forestry and fishery interactions*. Contribution 57, Institute of Forestry Resources, University of Washington, Seattle.
- Bolstad, P.V., and S. T. Gower. 1990. Estimation of leaf area index in fourteen southern Wisconsin forest stands using a portable radiometer. *Tree Physiology* 7:115-124.
- Borchert M., and M. Hibberd. 1984. Gradient analysis of a north slope montane forest in the western transverse ranges of southern California. *Madrono* 31(3):129-139.
- Bowers, J. E. and S. P. McLaughlin. 1982. Plant species diversity in Arizona. *Madrono* 29(4): 227-233.
- Burnett, M. R., P. V. August, J. H. Brown, and K. T. Killingbeck. 1998. Influence of geomorphic heterogeneity on diversity: I. a patch-scale perspective. *Conservation Biology* 12(2):363-370.
- Burns, R.M. and B.H. Honkala. 1990a. *Silvics of North America, Vol. 1, Conifers*. Washington DC: U.S.D.A. Forest Service Agriculture Handbook No. 654.
- Burns, R.M., and B. H. Honkala. 1990b. *Silvics of North America, Volume 2. Hardwoods*. Washington DC: U.S.D.A. Forest Service Agriculture Handbook No. 654.
- Busch, D.E., and S.D. Smith. 1995. Mechanisms associated with decline of woody species in riparian ecosystems of the southwestern U.S. *Ecological Monographs* 65:347-370.
- Busing, R. T. 1994. Canopy cover and tree regeneration in old-growth cove forests of the Appalachian Mountains. *Vegetatio* 115:19-27.
- Caley, M. J. and D. Schluter. 1997. The relationship between local and regional diversity. *Ecology* 78(1): 70-80.

- Catovsky, S. and F. A. Bazzazz. 2000. The role of resource interactions and seedling regeneration in maintaining a positive feedback in hemlock stands. *Journal of Ecology* 88:100-112.
- Collins, S. L, P. G. Risser, and E. L Rice. 1981. Ordination and classification of mature bottomland forests in northcentral Oklahoma. *Bulletin of the Torrey Botanical Club* 108(2):152-165.
- Collins, S.L. 1990. Habitat relationships and survivorship of tree seedlings in hemlock-hardwood forest. *Canadian Journal of Botany* 68:790-797.
- Connell, J. H. 1978. Diversity in tropical forests and coral reefs. *Science* 199:1302-1309.
- Connell, J.H. and E. Orias. 1964. The ecological regulation of species diversity. *American Naturalist* 98:399-414.
- Cornell, H.V. 1999. Unsaturation and regional influences on species richness in ecological communities: a review of the evidence. *Ecoscience* 6(3):303-315.
- Cowling RM, Rundel P.W. Lamont B.B., Arroyo M.K. and Arianoutsou, M. 1996. Plant diversity in Mediterranean-climate regions. *Trends in Ecology and Evolution* 11:362-66.
- Currie, D. J. and V. Paquin. 1987. Large-scale patterns of species richness of trees. *Nature* 329:326-327.
- Daubenmire, R. 1968. Soil moisture in relation to vegetation distribution in the mountains of northern Idaho. *Ecological Monographs* 49:431-438.
- del Moral, R. and R.S. Fleming. 1979. Structure of coniferous forest communities in western Washington: diversity and ecotope properties. *Vegetatio* 41:143-154.
- Dennis, N.B., M. L. Marcus, and H. Hill. 1984. Status and Trends of California Wetlands. A report to the California Assembly Resources Subcommittee. 125 pp.
- Diamond, J. 1988. Factors Controlling Diversity: Overview and Synthesis. *Annals of the Missouri Botanical Garden* 75:117-129.

- Dixon, M. D., M. G. Turner, and C. Jin. 2002. Riparian tree seedling distribution on Wisconsin River sandbars: controls at different spatial scales. *Ecological Monographs* 72(4): 465-485.
- Duncan, R.P. 1993. Flood disturbance and the coexistence of species in a lowland podocarp forest, south Westland, New Zealand. *Journal of Ecology* 81:403-416.
- Dykaar, B.B., and P. J. Wigington. 2000. Floodplain formation and cottonwood colonization patterns on the Willamette River, Oregon, USA. *Environmental Management* 25(1): 87-104.
- Dyrness, C. T.; Franklin, Jerry F.; Moir, W. H. 1974. A preliminary classification of forest communities in the central portion of the western Cascades in Oregon. Coniferous Forest Biome Bull. 4. Seattle, WA: University of Washington. 123 p.
- Feierabend, J. S. and J. M. Zelazny. 1987. Status Report on our Nation's Wetlands. National Wildlife Federation. Washington D. C. 46 pp.
- Fetherston, K. L., R. J. Naiman, and R. E. Bilby. 1995. Large woody debris, physical process, and riparian forest development in montane river networks of the Pacific Northwest. *Geomorphology* 13: 133-144.
- Fonda, R. W. 1974. Forest succession in relation to river terrace development in Olympic National Park, Washington. *Ecology* 55: 927-942.
- Franklin, J. F. ,and C. T. Dyrness. 1988. Natural Vegetation of Oregon and Washington. USDA Forest Service General Technical Report PNW-8.
- Framer, W. E. D. D. Peters and H. R. Pywell. 1989. Wetlands of the California Central Valley: Status and Trends. U.S. Fish and Wildlife Service. Portland, OR. 28 pp.
- Gentry, A. H. 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Annals of the Missouri Botanical Garden* 75:1-34.
- Giordano, P. and D. E. Hibbs. 1993. Morphological Response to Competition in Red Alder: The Role of Water. *Functional Ecology* 7:462-468.
- Gleason, H. A. 1926. The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* 53:7-26.

- Gleason, H. A. 1922. On the relation of species and area. *Ecology* 6:66-74.
- Gould, W. A. and M.D. Walker. 1997. Landscape-scale patterns in plant species richness along an arctic river. *Canadian Journal of Botany* 75:1748-1765.
- Grant, G. E., and F. J. Swanson, F. J. 1995. Morphology and processes of valley floors in mountain streams, western Cascades, Oregon. In: Costa, John E.; Miller, Andrew J.; Potter, Kenneth W.; Wilcock, Peter, eds. Natural and anthropogenic influences in fluvial geomorphology: the Wolman volume. Geophysical Monograph 89. Washington, DC: American Geophysical Union: 83-101.
- Grant, Gordon E.; Swanson, Frederick J., and Wolman, M. Gordon. 1990. Pattern and origin of stepped-bed morphology in high-gradient streams, Western Cascades, Oregon. *Bulletin of the Geological Society of America* 102: 340-352.
- Gray, A. N.; and T. A. Spies 1997. Microsite controls on tree seedling establishment in conifer forest canopy gaps. *Ecology* 78(8): 2458-2473.
- Gregory, S.V., F. J. Swanson, W. A. McKee, and K.W. Cummins. 1991. An ecosystem perspective of riparian zones. *Bioscience* 41 (8): 540-551.
- Grier, C. C. and S. W. Running. 1977. Leaf area of mature northwestern coniferous forests: relation to site water balance. *Ecology* 58:893-899.
- Grime J. P. 1977. Evidence of the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111:1169-1194.
- Grime, J.P. 1973. Control of species diversity in herbaceous vegetation. *Journal of Environmental Management* 1:151-167.
- Grubb, P. J. The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biological Review* 52: 107-145.
- Hack, J.T., and J. C. Goodlet. 1960. Geomorphology and forest ecology of a mountain region in the central Appalachians: U.S. Geological Survey Professional Paper 347, 66p.
- Harmon, M.E. and J. F. Franklin. 1989. Tree seedlings on logs in *Picea-Tsuga* forests of Oregon and Washington. *Ecology* 70(1):48-59.

- Harris, R. R. 1987. Occurrence of vegetation on geomorphic surfaces in the active floodplain of a Californian alluvial stream. *American Midland Naturalist* 18:393-405.
- Harrison, S., J. L. Viers and J. F. Quinn, 2000. Climatic and spatial patterns of diversity in the serpentine plants of California. *Diversity and Distributions* 6: 153-161.
- Hawk, G. M, and D. B. Zobel. 1974. Forest succession on alluvial landforms of the McKenzie River Valley, Oregon. *Northwest Science* 48(4):245-265.
- Helgerson, O. 1990. Heat damage in seedlings and its prevention. *New Forests* 37-42.
- Hibbs, D. E. , and A. L. Bower. 2001. Riparian forests of the Oregon Coast Range. *Forest Ecology and Management* 154:201-213.
- Hibbs, D. E. 1982. Gap dynamics in a hemlock-hardwood forest. *Canadian Journal of Forest Research* 12:522-527.
- Hibbs, D., and P. Giordano. 1996. Vegetation characteristics of alder-dominated riparian buffer strips in the Oregon Coast Range. *Northwest Science* 70:213-222.
- Hickman, J.C. Ed. 1993. *The Jepson Manual, Higher Plants of California*. University of California Press, Berkeley, CA. 1400 pp.
- Hitchcock C.L., and A. Cronquist. 1973. *Flora of the Pacific Northwest: An Illustrated Manual*. University of Washington Press, Seattle, WA.
- Holstein, G. 1984. California riparian forests: deciduous islands in an evergreen sea. *In California Riparian Systems*. University of California Press, Berkeley, University of California, Davis. pp. 1-13.
- Howell, J.T. 1957. The California flora and its province. *Leaflet of Western Botany* 5:109-124

- Hupp, C.R. 1986. Upstream variation in bottomland vegetation patterns, northwestern Virginia. *Bulletin of the Torrey Botanical Club* 113(4):421-430.
- Hupp, C.R., and W.R. Osterkamp. 1985. Bottomland vegetation distribution along Passage Creek, Virginia, in relation to fluvial landforms. *Ecology* 66(3): 670-681.
- Huston, M. 1979. A general hypothesis of species diversity. *American Naturalist* 113:81-101.
- Huston, M. 1994. Biological Diversity: the coexistence of species on changing landscapes. Cambridge University Press 681 pp.
- Huston, M. 1999a. Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. *Oikos* 86:393-401.
- Huston, M.A. 1999b. Forest productivity and diversity: Using ecological theory and landscape models to guide sustainable forest management. Pages 329-341 In Aguirre-Bravo, C. and C.R. Franco (compilers). North American Science Symposium: Toward a unified framework for inventorying and monitoring forest ecosystem resources. USDA Forest Service RMRS-P-12, 533 pp.
- Huston, M.A. and T. Smith. 1987. Plant succession: life history and competition. *American Naturalist* 130(2):168-198.
- Johnson, S. L. , F. J . Swanson, G. E. Grant, and S. M . Wondzell. 2000. Riparian forest disturbances by a mountain flood - the influence of floated wood. *Hydrological Processes* 00:1-20.
- Johnson, W.C. 1994. Woodland expansion in the Platte River, Nebraska: patterns and causes. *Ecological Monographs* 64:45-84.
- Keddy, P., and B. Shipley. 1989. Competitive hierarchies in herbaceous plant communities. *Oikos* 54:234-241.
- Kleidon, A. and H. A. Mooney. 2000 A global distribution of biodiversity inferred from climatic constraints: results from a process-based Modeling study. *Global Change Biology* 6(5): 507-524.

- Kolb, T. E., S. C. Hart, and R. Amundson. 1997. Boxelder water sources and physiology at perennial and ephemeral stream sites in Arizona. *Tree Physiology* 17:151-160.
- Kruskal, J. B. 1964. Nonmetric multidimensional scaling: a numerical method. *Psychometrika* 29: 115-129.
- Landsberg, J. J., and R. H. Waring. 1997. A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. *Forest Ecology and Management* 95:209-228.
- Latham, R. E. and R. E. Ricklefs. 1993a. Global patterns of tree species richness in moist forests: Energy-diversity theory does not account for variation in species richness. *Oikos* 67:325-333.
- Leopold L.B., M.G. Wolman, and J.P. Miller, 1964. *Fluvial Processes in Geomorphology*. Dover Publications, New York. 522 pp.
- MacArthur, R. H. and E. O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton University Press. Princeton, N. J.
- Magurran, A. E. 1988. *Ecological Diversity and Its Measurement*. Princeton University Press, Princeton.
- Major, J. 1951. A functional, factorial approach to plant ecology *Ecology* 32:392-412.
- Malanson, G. P. 1993. *Riparian Landscapes*. Cambridge University Press, Cambridge, UK. 296 pp.
- Marshall, J. D. and R. H. Waring. 1986. Comparison of methods of estimating leaf-area index in old-growth Douglas-fir. *Ecology* 67:975-979.
- Mason, H. L. and J.H. Langenheim. 1957. Language analysis and the concept environment. *Ecology* 38:325-340.
- Mather, P. M. 1976. *Computational Methods of Multivariate Analysis in Physical Geography*. J. Wiley and Sons, London. 532 pp.
- Maftsoft, Inc. 2000. SPLUS Version 6.0 for Windows.

- McCune, B. and M. J. Mefford. 1999. PC Ord for Windows. Multivariate Analysis of Ecological Data, Version 4.20. MJM Software, Gleneden Beach, Oregon, USA
- McLaughlin, S. P. 1989. Natural floristic areas in the western United States. *Journal of Biogeography* 16: 239-248.
- Means, Joseph E. 1982. Developmental history of dry coniferous forests in the central western Cascade Range of Oregon. In: Means, Joseph E., ed. Forest succession and stand development research in the Northwest: Proceedings of the symposium; 1981 March 26; Corvallis, OR. Corvallis, OR: Forest Research Laboratory, Oregon State University: 142-158.
- Minore, D. 1979. Comparative autecological characteristics of northwestern tree species: a literature review. USDA Forest Service General Technical Report GTR-PNW-87.
- Minore, D. and H.G. Weatherly 1994. Riparian trees, shrubs, and forest regeneration in the coastal mountains of Oregon. *New Forests* 8:249-263.
- Mitsch, W.J., and J.G. Gosselink. 2000. *Wetlands*. 3rd edition, J. Wiley & Sons, New York.
- Monteith, J.L. 1965. Evaporation and the environment. *Symposium of the Society for Experimental Biology* 19: 205-234.
- Montgomery, D. R.. 1999. Process domains and the river continuum. *Journal of the American Water Resources Association* 35: 397-410.
- Mount J. 1995. *California Rivers and Streams: Conflict between Fluvial Process and Land Use*. University of California Press. Berkeley. 359 pp.
- Mouw, J.E. B. and P. A. Alaback. 2002. Putting floodplain hyperdiversity in a regional context. an assessment of terrestrial-floodplain connectivity in a montane environment. *Journal of Biogeography* 30:87-103.
- Naiman, R. J. R.E. Bilby, and P.A. Bisson. 2000. Riparian ecology and management in the Pacific coastal rainforest. *BioScience* 50(11):996-1011.
- Naiman, R. J., H., DeCamps, and M. Pollock. 1993. The role of riparian corridors in maintaining regional biodiversity. *Ecological Applications* 3(2):209-212.

- Nakamura, Futoshi; Swanson, Frederick J.; Wondzell, Steven M. 2000. Disturbance regimes of stream and riparian systems--a disturbance-cascade perspective. *Hydrological Processes* 14: 2849-2860.
- Nichols, W. F., K. T. Killingbeck, and P. V. August. 1998. The influence of geomorphic heterogeneity in biodiversity: II. a landscape perspective. *Conservation Biology* 12(2):371-379.
- Nierenberg, T., 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.
- Nilsson, C., G. Grelsson, M. Johansson, and Ulf Sperens. 1989. Patterns of species richness along riverbanks. *Ecology* 70(1):77-84.
- O'Brien, E.M. 1998. Water-energy dynamics, climate, and predictions of woody plant species richness: an interim general model. *Journal of Biogeography* 25:379-398.
- O'Neill, R. V., D. L. De Angelis, J.B. Waide, and T. F. H. Allen. 1986. A hierarchical concept of ecosystems. Princeton University Press. Princeton New Jersey, USA.
- Ohmann, J. and T. Spies, 1998. Regional gradient analysis and spatial pattern of woody plant communities of Oregon Forests. *Ecological Monographs* 68(2): 151-182.
- Orr, E. L. , and W. N. Orr. 1999. *Geology of Oregon*. Kendall/Hunt Publishing, Dubuque, IA (fifth edition).
- Pabst, R.J. , and T. Spies. 1998. Distribution of herbs and shrubs in relation to landform and canopy cover in riparian forests of coastal Oregon. *Canadian Journal of Botany* 76: 298-315.
- Pabst, R.J. , and T. Spies. 2002. Ten years of vegetation succession on a debris flow deposit in Oregon. *Journal of the American Water Resources Association* 37(6):1693-1708.
- Pabst, R.J. , and T.A. Spies. 1998. Distribution of herbs and shrubs in relation to landform and canopy cover in riparian forests of coastal Oregon. *Canadian Journal of Botany* 76: 298-315.

- Pabst, R.J. and Spies, T.A. 1999. Structure and composition of unmanaged riparian forests in the coastal mountains of Oregon, U.S.A. *Canadian Journal of Forest Research* 29:1557-1573.
- Pattee, H.H. 1973. *Hierarchy Theory: the challenge of complex systems*. George Braziller, Inc. New York. 156 pp.
- Patten, D. T. 1998. Riparian ecosystems of semi-arid North America: diversity and human impacts. *Wetlands* 18(4):498-512.
- Pickett, S. T. A., and P. S. White. 1985. *The ecology of natural disturbance and patch dynamics*. Academic Press, Orlando, Florida, USA.
- Pojar, J., K. Klinka and D.V. Meidinger. 1987. Biogeoclimatic Ecosystem Classification in British Columbia. *Forest Ecology and Management* 22: 119-154.
- Pollock, M. M., R.J. Naiman, T. A. Hanley. 1998. Plant species richness in forested and emergent wetlands- a test of biodiversity theory. *Ecology* 79:94-105.
- Preston, F. W. 1960. Time and space and the variation of species. *Ecology* 41:611-627.
- Rich, P.M. 1989. A manual for analysis of hemispherical canopy photography. Los Alamos National Laboratory Report LA-11733-M.
- Richerson, P. J. and K. Lum. 1980. Patterns of plant species richness in California: relation to weather and topography. *American Naturalist* 116:504-536.
- Ricklefs R. E. 1987. Community diversity: relative roles of local and regional Processes. *Science* 235: 167-171.
- Roberts, M R and F S Gilliam. 1995. Patterns and mechanisms of diversity in forested ecosystems: implications for forest management. *Ecological Applications* 5:969-977.
- Robertson, K. M., and C. K. Augsberger. 1999. Geomorphic processes and spatial patterns of primary forest succession on the Bogue Chitto River, USA. *Journal of Ecology* 87(6): 1052-1063.

- Rood, S. B., A. R. Kalischuk, and J. M. Maloney. 1998. Initial cottonwood seedling recruitment following the flood of the century of the Oldman River, Alberta, Canada. *Wetlands* 18(4): 557-570.
- Rood, S. B. and J. M. Mahoney. 1990. Collapse of riparian poplar forests downstream from dams in western prairies: probable causes and prospects for restoration. *Environmental Management* 14:451-464.
- Rosenzweig, R. L. 1995. Species diversity in space and time. Cambridge University Press, Cambridge.
- Running, S.W., Nemani, R.R., and R.D. Hungerford. 1987. Extrapolation of synoptic meteorological data in mountainous terrain and its use for simulating forest evapotranspiration and photosynthesis. *Canadian Journal of Forest Research* 17: 472-483.
- Sakai, T. T. Hiroshi, W. Suzuki, H. Nomuya, T. Kanazashi, S. Iida, and T. Nakashizuka. 1999. Riparian disturbance and community structure of a *Quercus-Ulmus* forest in central Japan. *Plant Ecology* 140:99-109.
- Sarr, D.A., D.E. Hibbs, and M. A. Huston. (in press). A hierarchical perspective of plant diversity. *Quarterly Review of Biology*.
- 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(4):960-979.
- Schrader, B. 1998. Structural Development of Late Successional Forests in the Central Oregon Coast Range: Abundance, Dispersal, and Growth of Western Hemlock (*Tsuga heterophylla*) Regeneration. PhD Dissertation, Oregon State University, Corvallis. 175 pp.
- Scott, M.L., J.M. Friedman, and G. T. Auble., 1996. Fluvial Processes and the establishment of bottomland trees. *Geomorphology* 14:327-339.
- Shmida, A. and M.V. Wilson. 1985. Biological determinants of species diversity. *Journal of Biogeography* 12:1-20.
- Smith, T. and M. Huston. 1989. A theory of the spatial and temporal dynamics of plant communities. *Vegetatio* 83:49-69
- Spies, T. A., and J.F. Franklin. 1989. Gap characteristics and vegetation response in coniferous forests of the Pacific Northwest. *Ecology* 70(3):543-545.

- Spomer, G. G. 1973. The concept of "interaction" and "operational environment" in environmental analyses. *Ecology* 54(1):200-204.
- Stebbins G. L., and J. Major. 1965. Endemism and speciation in the California flora. *Ecological Monographs* 35(1):1-35.
- Stevens, M. H. H., and W.P. Carson. 2002. Resource quantity, not resource heterogeneity, controls diversity. *Ecology Letters* 5:420-426.
- Stewart, G. H. 1988. The influence of canopy cover on understory development in forests of the western Cascade Range, Oregon, USA. *Vegetatio* 76: 79-88.
- Stromberg, J. C., J. Fry, and D. T. Patten. 1997 Marsh development after large floods in an alluvial, arid river. *Wetlands* 17(2) 292-300.
- Swanson, F. J., S.L. Johnson, S.V. Gregory, and S.A. Acker. 1998. Flood disturbance in a forested mountain landscape: interactions of land use and floods. *Bioscience* 48(9):681-688.
- Systat Software, Inc. 2002. SYSTAT Version 10.2 for Windows.
- Swanson, F. J.; Kratz, T. K.; Caine, N., and Woodmansee, R. G. 1988. Landform effects on ecosystem patterns and processes. *BioScience* 38:(2) 92-98.
- Tabacchi, E., and A. M. Planty-Tabacchi, M. J. Salinas, and Henri Decamps. 1996. Landscape Structure and Diversity in Riparian Plant Communities: A Longitudinal Comparative Study. *Regulated Rivers: Research and Management* 12: 367-390.
- Tappeiner II, J.C., J. C. Zasada, P. Ryan, and M. Newton. 1991. Salmonberry clonal and population structure, the basis of a persistent cover. *Ecology* 72(2):609-618.
- Thomas, S. C., C. B. Halpern, D. A. Falk, D. A. Liguori, and K. A. Austin. 1999. Plant diversity in managed forests: understory responses to thinning and fertilization. *Ecological Applications* 9:864-879.
- Thornton, P.E., S.W. Running, and M.A. White, 1997. Generating surfaces of daily meteorological variables over large regions of complex terrain. *Journal of Hydrology* 190:214-251.

- Tilman, D. 1982. *Resource competition and community structure*. Princeton University Press. Princeton University, N.J.
- Tilman, D. 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. *Ecological Monographs* 57(3): 189-214.
- Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75:2-16.
- Tyree, M. T., K. J. Kolb, S. B. Rood., and S. Patino. 1994. Vulnerability to drought-induced cavitation of riparian cottonwoods in Alberta: a possible factor in the decline of the ecosystem? *Tree Physiology* 14:455-466.
- USDA (Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory). 2002. Fire Effects Information System, [Online]. Available: <http://www.fs.fed.us/database/feis/> [Accessed Feb. 10, 2002].
- USDA and USDI 1994b. Record of Decision for amendments to Forest Service and BLM planning documents within the range of the northern spotted owl. USDA Forest Service Regional Office. Portland, OR.
- Vankat, J. L. 1982. A gradient perspective on the vegetation of Sequoia National Park, California. *Madrono* 29(3):200-214.
- Vannote, R. L., G. W. Minshall, K.W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. 'The River Continuum Concept'. *Canadian Journal of Fisheries and Aquatic Science* 7:130-137.
- Veblen, T. T. 1989. Tree regeneration responses to gaps along a trans-Andean gradient. *Ecology* 70(3):541-543.
- Veblen, T. T. 1992. Regeneration Dynamics. Pp 153-191 In: Plant Succession: Theory and Prediction. D. C. Glenn-Lewing, R. K. Peet, and T. T. Veblen (eds). Chapman and Hall, London.
- Waring, R. H., N. C. Coops, J. L. Ohmann, and D. A. Sarr. 2002. Interpreting woody plant richness from seasonal ratios of photosynthesis. *Ecology* 83(11):2964-2970.
- Waring, R. H. 1969. Forest plants of the eastern Siskiyou: their environmental and vegetational distribution. *Northwest Science* 43:1-17.
- Waring, R. H. and J. F. Franklin 1979. Evergreen coniferous forests of the Pacific Northwest. *Science* 204:1380-1386.

- Waring, R. H. and S. W. Running. Forest Ecosystems: Analysis at Multiple Scales, 2nd Edition. Academic Press, 1998
- Waring, R. H., and B. D. Cleary. 1967. Plant moisture stress: evaluation by pressure bomb. *Science* 155:1248-1254.
- Waring, R. H., and J. Major. 1964. Some vegetation of the California Coastal Redwood Region in relation to gradients of moisture, nutrients, light and temperature. *Ecological Monographs* 34:167-215.
- Wells, G. and D. Anzinger. 2001. *Lewis and Clark Meet Oregon's Forests: Lessons from Dynamic Nature*. Oregon Forest Resources Institute, Portland, Oregon. 223 p.
- Whitmore, T. C. 1989. Canopy gaps and the two major groups of forest trees. *Ecology* 70(3):536-538.
- Whittaker, R.H. 1956. Vegetation of the Great Smoky Mountains. *Ecology* 26: 1-80.
- Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* 30:279-338.
- Whittaker, R. J. Willis, K.J., and R. Field. 2001. Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography* 28:453-470.
- Whittaker, R.H. 1965. Dominance and diversity in land plant communities. *Science* 147: 250-259.
- Wilson, M. V., and A. Shmida. 1984. Measuring beta diversity with presence-absence data. *Journal of Ecology* 72:1055-1064.
- Wimberly, M. C. and T. A. Spies. 2001. Influences of environment and disturbance on forest patterns in coastal Oregon watersheds. *Ecology* 82(5):1443-1459.
- Zobel, D. B., A. McKee, and G. Hawk. 1976. Relationships of environment to composition, structure, and diversity of forest communities of the central western Cascades of Oregon. *Ecological Monographs* 46:135-156.

APPENDIX

Appendix 1. Pairwise predictions of regeneration patterns for each functional group based on regeneration model (Figure 4.2b) for gap and forest sites in each watershed and for interbasin comparisons of gap and forest sites. All predictions refer to the expected (EXP.) relationship of seedling abundances in the first compared to second member of the pair. Observed relationships (OBS.) are to the right of the expected column for each functional group. N/A means no seedlings expected in either of pair or no seedlings were observed for comparison.

COMPARISONS			FUNCTIONAL GROUP 1		FUNCTIONAL GROUP 2		FUNCTIONAL GROUP 3		FUNCTIONAL GROUP 4		FUNCTIONAL GROUP 5	
			EXP	OBS.	EXP.	OBS.	EXP.	OBS.	EXP.	OBS.	EXP.	OBS.
<u>GAP/FOREST COMPARISONS</u>												
APPLEGATE	GAP	FOREST	+	+	-	-	-	+	-	+	+	+
SOUTH UMPQUA	GAP	FOREST	+	+	-	-	-	+	+	+	+	N/A
McKENZIE	GAP	FOREST	+	+	-	-	+	+	+	+	N/A	N/A
ALSEA	GAP	FOREST	+	+	+	+	+	+	+	+	N/A	N/A
<u>INTERBASIN COMPARISONS</u>												
GAPS	APPLEGATE	UMPQUA	-	-	-	-	-	+	-	+	+	+
GAPS	UMPQUA	McKENZIE	-	-	-	-	-	+	+	+	+	N/A
GAPS	McKENZIE	ALSEA	-	-	-	+	+	+	+	+	N/A	N/A
FOREST	APPLEGATE	UMPQUA	-	-	-	-	-	-	+	+	+	+
FOREST	UMPQUA	McKENZIE	-	+	-	-	+	+	+	+	N/A	N/A
FOREST	McKENZIE	ALSEA	-	+	+	+	+	+	+	+	N/A	N/A
GAPS	APPLEGATE	McKENZIE	-	-	-	-	-	+	+	+	+	+
GAPS	APPLEGATE	ALSEA	-	-	-	-	-	+	+	+	+	+
FOREST	APPLEGATE	McKENZIE	-	-	-	-	+	+	+	+	+	+
FOREST	APPLEGATE	ALSEA	-	-	-	+	+	+	+	+	+	+
GAPS	UMPQUA	McKENZIE	-	-	-	-	-	+	+	+	+	N/A
GAPS	UMPQUA	ALSEA	-	-	-	+	+	+	+	+	+	N/A
FOREST	UMPQUA	McKENZIE	-	+	-	-	+	+	+	+	N/A	N/A
FOREST	UMPQUA	ALSEA	-	+	+	+	+	+	+	+	N/A	N/A