AN ABSTRACT OF THE DISSERTATION OF

Michael C. Wimberly for the degree of Doctor of Philosophy in Forest Science presented on May 14, 1999. Title: Watershed-Scale Vegetation Patterns in a Late-Successional Forest Landscape in the Oregon Coast Range.

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Knowledge about vegetation patterns and ecological processes in unmanaged, late-successional watersheds is needed to provide a foundation for forest management strategies aimed at conserving native biodiversity. I examined influences of environmental variability and disturbance history on forest structure and composition in the Cummins Creek Wilderness, located on the central Oregon coast. Climatic and topographic variables explained the majority of hillslope community composition, while fire history explained most of the variability in hillslope forest structure. Forest structure and composition in riparian areas was related to a climatic gradient as well as position in the stream network. The abundance of two fire-sensitive species, *Tsuga heterophylla* (western hemlock) and *Picea sitchensis* (Sitka spruce), decreased with distance from old-growth patches, possibly reflecting a seed dispersal gradient that occurred following fires 80 to 140 years ago.

I developed predictive maps of understory conifer patterns using remote sensing, aerial photographs, digital elevation models and stream maps. I predicted *P. sitchensis* regeneration based on distance from the coast and topography, and *T. heterophylla* regeneration based on crown size, percent hardwood composition, topography, and distance from old-growth patches. Although I found statistically significant relationships between

understory patterns and GIS predictor variables, the models explained only low to moderate amounts of the overall variability.

Landscape-scale simulations of *T. heterophylla* showed that population expansion through gap-phase recruitment was limited by short seed dispersal distances in closed-canopy forests, the requirement for canopy gap disturbances to facilitate overstory recruitment, and the lag between recruitment and reproduction. Although fine-scale habitat features can influence the amount of regeneration in a gap when seed sources are present, the fire regime may ultimately control the abundance of *T. heterophylla* at the landscape scale through dispersal limitations. Brief increases in fire frequency can cause a sustained decrease in the amount of *T. heterophylla* on the landscape once fire frequency is reduced below a threshold value.

Our results emphasize the complexity and diversity of forest vegetation at the watershed scale. Environmental variability, disturbance history, and dispersal limitations have all played a role in creating the current landscape patterns in the Cummins Creek Wilderness.

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Watershed-Scale Vegetation Patterns in a Late-Successional Forest Landscape in the Oregon Coast Range

by

Michael C. Wimberly

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

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Michael C. Wimberly, Author

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TABLE OF CONTENTS

Page

CHAPTER 1: General Introduction 1

Background 1

Overview of the Study 7

CHAPTER 2: Assessing the Influences of Disturbance History and Environmental Variability on Forest Structure and Composition in Coastal Oregon Watersheds 14

Abstract 15

Introduction 16

Study Area 22

Methods 25
- Vegetation Data 25
- Environmental Data 27
- Disturbance Data 28
- Data Analyses 30

Results 34
- Disturbance History 37
- Differences Between Riparian and Hillslope Forests 34
- Species Composition Patterns 41
- Forest Structure Patterns 50
- Relative Importance of Disturbance and Environment 56

Discussion 58
- Recent Fire History 58
- Riparian Forests 60
- Landscape Patterns 62
- Implications for Management and Conservation 66

CHAPTER 3: Predicting Landscape Patterns of Understory Conifers Using Field Plots, Remote Sensing, and Digital Elevation Models 69

Abstract 70

Introduction 71

Study Area 76

Methods 77
- Field Data Collection 77

TABLE OF CONTENTS (CONTINUED)

Page

GIS Data Layers 80
Predictive Models 84
Correlation with Stand Variables 86

Results 87

Discussion 101
Validity of the Modeling Approach 101
Remnants and the Role of Disturbance 103
Riparian Areas 105
Fate of Hardwood Patches 106

Conclusions 108

CHAPTER 4: Modeling the Temporal and Spatial Dynamics of a Late-Successional, Fire-Sensitive Tree Species 110

Abstract 111

Introduction 111
Conceptual Framework 114
Modeling Approach 118

Methods 119
Model Description 119
Model Analysis 125

Results 127

Discussion 134

Conclusions 143

CHAPTER 5: Conclusions 145

Overview 145

Conclusions 149

BIBLIOGRAPHY 152

APPENDIX 165

LIST OF FIGURES

Figure		Page
1.1	Conceptual model of watershed-scale vegetation patterns	8
1.2	Location of the Cummins Creek Wilderness	10
2.1	Map of field sites in the Cummins Creek Wilderness.	23
2.2	Age class distribution by topographic position	35
2.3	Redundancy analysis biplot for hillslope species composition.	43
2.4	Basal area per hectare of a) *T. heterophylla* and b) *P. sitchensis* as a function of distance from the nearest old-growth patch.	46
2.5	Redundancy analysis biplot for riparian species composition	48
2.6	Overstory species composition as a function of distance from the coast for a) riparian areas and b) hillslopes.	49
2.7	Redundancy analysis biplot for hillslope forest structure.	51
2.8	Redundancy analysis biplot for riparian forest structure.	55
2.9	Percentage of the total variation explained (TVE) accounted for by disturbance and environment variables in the redundancy analysis ordinations.	57
3.1	Maps of field site locations in the Cummins Creek Wilderness with raw data values	78
3.2	Maps of independent variables used to develop the predictive maps, including a) distance from remnant old-growth patches, b) percent broadleaf cover and c) the riparian network	83
3.3	Percentage of sites with *P. sitchensis* regeneration as a function of a) distance from the coast and b) slope position	89
3.4	*P. sitchensis* regeneration density as a function of distance from the coast for riparian areas versus hillslopes.	89
3.5	Maps of predicted conifer patterns generated using a fixed cutoff to predict presence/absence and the mean regression response to predict density. a) *P. sitchensis* advance regeneration, b) *T. heterophylla* advance regeneration and c) *T. heterophylla* understory trees. Shaded areas represent cut stands that were excluded from our analysis.	83

LIST OF FIGURES (CONTINUED)

Figure | Page

3.6 Proportion of sites with *T. heterophylla* regeneration as a function of a) distance from the nearest old-growth remnant patch, b) percent broadleaf cover, c) overstory conifer crown diameter and d) percent slope. 92

3.7 *T. heterophylla* advance regeneration density as a function of a) distance from the coast for low-order riparian areas versus other landform types, b) slope position and c) landform....93

3.8 Proportion of sites with understory *T. heterophylla* trees as a function of a) distance from remnants and b) percent broadleaf cover....95

3.9 *T. heterophylla* advance regeneration density as a function of a) percent broadleaf cover, b) distance from old-growth remnant patches and c) landform....96

3.10 Maps of predicted conifer patterns generated using probabilistic predictions of presence/absence and incorporating random error into the prediction of density. a) *P. sitchensis* advance regeneration, b) *T. heterophylla* advance regeneration c) *T. heterophylla* understory trees....97

4.1 State and transition diagram for the *T. heterophylla* patch dynamics model....120

4.2 Probability of *T. heterophylla* establishment as a function of distance from seed source when FDISP=0.005....122

4.3 Expected cumulate proportion of the landscape with canopy gaps as a function of time since fire for three values of the gap return interval parameter (GRI)....122

4.4 Results from a single model run with FRI=300, FSEV=0.9, PATCH=1, GRI=150, GREC=0.5, BDISP=0.0075....128

4.5 Results from a single model run with FRI=300, FSEV=0.9, PATCH=6, GRI=150, GREC=0.5, BDISP=0.0075....131

4.6 Results from a single model run with FRI=300, FSEV=0.99, PATCH=6, GRI=150, GREC=0.5, BDISP=0.0075....132

4.7 Locally weighted regression models predicting the proportion of cells on the landscape containing *T. heterophylla* as a function of a) fire return interval (years), b) fire severity (proportion of landscape burned), c) number of remnant patches, d) gap return interval (years), e) probability of establishment in canopy gaps and f) probability of background dispersal independent of seed source locations....133

LIST OF FIGURES (CONTINUED)

Figure | Page

4.8 Contour plots of locally weighted regression models predicting *T. heterophylla* landscape frequency as a function of a) fire severity (FSEV) and remnant gap recruitment probability (GREC), and b) fire severity (FSEV) and gap return interval (GRI). 135

4.9 Contour plots of locally weighted regression models predicting *T. heterophylla* landscape frequency as a function of a) fire severity (FSEV) and remnant patch density (PATCH), and b) fire severity (FSEV) and fire return interval (FRI) 136

4.10 Differences between the mean of 100 treatment runs and the mean of 100 control runs computed at 50-year intervals for four different time series of fire frequencies 137

LIST OF TABLES

Table		Page
2.1	Mean values (with standard errors in parentheses) of stand age, stand structure variables, tree species basal area, and shrub species cover for hillslope and riparian areas.	38
2.2	Percent of hillslope and riparian sites falling within each disturbance category.	39
2.3	Regression models of disturbance variables as a function of physiographic variables at riparian and hillslope sites	39
2.4	Comparison of mean regeneration density (with standard error in parentheses) on hillslopes and riparian areas by distance from the coast	42
2.5	Species composition of seedling and saplings computed as a percentage of the total density of seedlings or saplings within each landscape unit	42
2.6	Correlation of species, environment, and disturbance variables with the first two axes of the hillslope and riparian community composition RDAs	44
2.7	Correlation of structure, environment, and disturbance variables with the first two axes of the hillslope and riparian forest structure RDAs	52
3.1	Potential explanatory variables used to develop predictive models for understory conifer patterns.	81
3.2	Binary generalized linear models used to predict presence/absence of understory conifers.	88
3.3	Linear regression models used to predict density of understory conifers at the sites where they were present.	90
3.4	Correlation between GIS variables used in the predictive models and stand attributes measured in the field plots	99
3.5	Mean values of stand attributes measured in the field plots for each of three landscape categories used in the predictive models	100
4.1	Parameter values used in the model analysis	126

Watershed-Scale Vegetation Patterns in a Late-Successional Forest Landscape in the Oregon Coast Range

CHAPTER 1: General Introduction

Background

Human activities have brought considerable change to Oregon's Coast Range forests since the first European settlers arrived in the mid-19th century. During the latter half of the 19th century and the first decades of the 20th century, burning by settlers in combination with the warm, dry climate at the end of the Little Ice Age led to increased fire frequencies across much of the region (Impara 1997, Weisberg 1998). Following this period, enhanced fire suppression efforts greatly reduced the occurrence of fires, even in areas where frequent, low-severity burns were an integral element of historical forest dynamics. Timber harvesting and intensive forest management practices in the latter half of the twentieth century have also changed the Coast Range landscape by reducing the amount of old forests on the landscape (Wimberly et al. in press) and perforating and fragmenting the remaining late-successional forests (Spies et al. 1994, Means et al. 1996, Ripple et al. in press).

These rapid and widespread changes have led to concern for the viability of populations of native species, particularly those associated with late-successional and old-growth forests (FEMAT 1993). Efforts are currently underway to develop new landscape management strategies that attempt to preserve native biodiversity while still maintaining some level of commodity production (Oliver 1992, FEMAT 1993, Cissel et al. 1998). Some threatened and endangered species such as the Northern Spotted Owl (*Strix occidentalis cauriana*) have been the subject of intensive research, which has resulted in the development of detailed single-species conservation plans (Thomas et al. 1990). There are many other

native species, however, for which detailed information on demography and habitat requirements is not available. Because of our limited knowledge and resources, developing and implementing individual management plans for every species is not feasible at this time. Instead, the "coarse-filter" approach has been proposed as an alternative method for conserving native biodiversity at the landscape scale (Hunter 1990). This method entails preserving the full range of natural diversity at the community level, based on the assumption that a representative array of habitats will be sufficient to meet the needs of most species.

Implementing a coarse-filter conservation strategy requires some characterization of the range of habitats that would be expected in a naturally functioning forest ecosystem. One way to obtain this information is by studying unmanaged wilderness landscapes. Wilderness areas can serve as baselines against which to compare landscapes altered by humans, and also as potential targets for ecosystem restoration (Franklin 1987). In addition to simply describing the range of community conditions in these landscapes, it is also important to relate community patterns to the underlying ecological processes that shape them. Understanding these pattern-process relationships provides the fundamental framework for landscape restoration strategies, and also serves as a basis for understanding how landscapes will change in the future.

Environmental constraints, disturbances, and biotic processes have been characterized as the three main drivers of pattern formation in natural landscapes (Levin 1978, Urban et al. 1987). Several fundamental ecological principles provide the scientific basis for understanding these processes and their influences on forest ecosystems. A species' response to the environment, for example, is often conceptualized as a fundamental niche that encompasses its range of tolerance to various environmental factors such as light, moisture, and temperature (Hutchinson 1957). The narrower, realized niche encompasses the range of

conditions that the species will tolerate when competition from other species is also taken into account. Different species tend to occupy distinctive environmental niches, and community composition thus changes with environmental conditions that vary spatially as a function of elevation, topography, and soil conditions. These community patterns are often characterized as a series of overlapping niches arrayed along one or more environmental gradients (Whittaker 1967).

In the Oregon Coast Range, for example, the coast-to-inland climatic gradient has a strong influence on forest community composition. Mean annual precipitation increases with distance from the coast as air masses are lifted over the Coast Range Mountains, but decreases again on east side of the Coast Range crest (Hemstrom and Logan 1986, Franklin and Dyrness 1988). The annual range of temperature variability also changes with distance from the coast, with inland sites tending to have warmer summers and colder winters than coastal areas. Summer fog is common along the coast, and may add to precipitation by condensing in tree crowns (Franklin and Dyrness 1988). Characteristic tree species change along this gradient, ranging from *Picea sitchensis* (Sitka spruce) and *Tsuga heterophylla* (western hemlock) in the cool, moist coastal regions to *Quercus garryana* (Oregon white oak) and *Arbutus menziesii* (Pacific madrone) along the warmer and dryer Willamette valley margin (Ohmann and Spies 1998). Finer-scale topographic variation related to hillslope position and aspect also influences moisture availability. Dry sites on upper hillslopes and exposed south aspects often support different plant communities than moister sites on lower hillslopes and sheltered north aspects (Hemstrom and Logan 1986).

Disturbances such as fires, floods, and windstorms create a landscape mosaic of different-aged vegetation patches. Disturbance regimes are stochastic processes, and the occurrence and location of a particular disturbance on the landscape may not be predictable at

any given point in time. When viewed at a larger scale, however, the finer-scale variability may average out and the behavior of the aggregate landscape can be somewhat predictable (Turner et al 1993). Elements of the disturbance regime can also be linked to environmental constraints. For example, ridgelines and river corridors may serve as firebreaks that limit fire spread (Agee 1993). Windthrow may be more likely to occur on shallow soils, or slopes exposed to prevailing winds (Ruth and Yoder 1953, Sinton 1996), and the effect of floods on streamside vegetation may depend on local geomorphic channel constraints (Hupp 1982, Grant and Swanson 1995).

Past disturbances have played a major role in shaping the current Coast Range landscape. Over the past several millennia, fire return intervals in the Central Coast Range have ranged from 200 to 300 years (Impara 1997, Long et al. 1998). Several particularly large and destructive fires have occurred within the last 150 years. These include the Nestucca (120,000 ha in 1848), Siletz (325,000 ha in 1849), Yaquina (195,000 ha in 1853) and Tillamook (95,000 ha in 1933) fires (Loy et al. 1976). Wind is also a prevalent disturbance agent, particularly near the coast (Ruth and Yoder 1953). Windthrow typically creates disturbed patches ranging from a single tree up to several hectares in size (Taylor 1990). Infrequent, high-severity wind events such as the Columbus Day storm of 1962 have the potential to disturb even larger areas distributed across the entire region (Hemstrom and Logan 1986). As in other portions of the Pacific Northwest, flooding often occurs during the rainy winter months and can kill riparian vegetation by undercutting, uprooting, or battering with flood-borne debris (Swanson et al. 1998). Saturated soils during high rainfall events can trigger other disturbances such as landslides and debris flows (Benda 1990).

Following these disturbances, the biotic processes of dispersal, establishment, growth, and mortality influence the type of forest community that establishes and the manner in which

it changes over time. Dispersal by wind or animals can potentially carry tree seeds hundreds to thousands of meters from their source (Howe and Smallwood 1982). Because seeds of most tree species do not persist in the soil seed bank (Silvertown and Lovett Doust 1993), the mix of species that establishes after a disturbance is strongly linked to the abundance and spatial pattern of remnant seed sources that are present (Oliver and Larson 1990). A species may not occur in otherwise suitable habitat if propagule availability is limited by the absence of a seed source within the species' dispersal range (Clark et al. 1998). Conversely, a species may be able to dominate a community in marginal habitat if it has a large amount of seed available relative to other species, allowing it to saturate potential safe-sites with propagules (Horn 1981). Interactions among disturbance, dispersal, and competitive processes have a strong impact on the temporal and spatial patterns of species across a landscape (Green 1989).

In many cases, changes in species composition after a major disturbance follow somewhat predictable developmental pathways. A number of mechanisms have been proposed to explain plant succession (Gleason 1926, Clements 1936, Egler 1954). Connell and Slatyer (1977) synthesized many of these ideas into a conceptual framework that encompassed three major successional models: facilitation, tolerance, and inhibition. The facilitation model emphasizes feedback mechanisms in which early-successional species modify the environment to make it more favorable for the establishment of late-successional species (Clements 1936). The second, tolerance model focuses on species life-history characteristics and competition for resources as the primary mechanisms driving successional change (Gleason 1926, Noble and Slatyer 1980). The third, inhibition model emphasizes an initial floristics view in which the first group of plants to colonize a site will continue to dominate by preventing successive colonization by other species (Egler 1954).

The fact that most of the tree species found in Pacific Northwest forests have the ability to establish following a large disturbance (Franklin and Hemstrom 1981) suggests that the facilitation model is inappropriate for describing successional dynamics (Connell and Slatyer 1977). Shorter lived hardwood species such as *Alnus rubra* (red alder) and *Prunus emarginata* (bitter cherry) senesce within a century, leaving stands dominated by longer lived conifers such as *Pseudotsuga menzeisii* (Douglas-fir), *Picea sitchensis* (Sitka spruce), and *Tsuga heterophylla* (western hemlock). Over longer time frames, conifer mortality also inevitably occurs. Shade-tolerant species such as *T. heterophylla* possess physiological and morphological plasticity that allows them to establish and survive in the forest understory under low light conditions, but then rapidly increase growth in response to canopy gaps created by the death of overstory trees (Oliver 1976, Tucker and Emmingham 1977). These gradual shifts toward long-lived species and species that can establish and survive in the understory environment incorporate elements of both the inhibition and tolerance models of succession (Connell and Slatyer 1977).

Characteristic pathways of structural dynamics often parallel these floristic changes. Young, dense stands of small trees have thick canopy cover and allow little light to penetrate to the forest floor (Oliver 1981, Peet and Christenson 1987). These young forests may have high density of snags and high volumes of down wood if these were left as residuals from the previous stand (Agee and Huff 1987, Spies et al. 1988). As the forest ages and trees grow in height, a network of linear openings develops at the margins of tree crowns (Oliver 1990) and the death of individuals and small patches of overstory trees create canopy gaps (Spies et al. 1990, Spies 1997). Gap formation increases the amount of light moisture and other resources in the forest understory, providing opportunities for establishment and recruitment of shade-tolerant trees into the overstory (Christy 1986, Spies et al. 1990, Alaback and Tappeiner

1991). Levels of down wood are often low during this phase because residual wood from the previous stand has begun to decay, but the current stand has not yet contributed many large boles to the snag and down wood pools (Agee and Huff 1987, Spies et al. 1988). Tree growth, establishment and death all continue as the forest ages, facilitating the development of the large live trees, complex canopy structure and accumulations of snags and down logs characteristic of old growth (Franklin and Spies 1991, Spies and Franklin 1991). If stand development continues without another major disturbance, the forest will eventually develop the "true old growth" or "shifting mosaic" structure in which all trees in the initial cohort have died and been replaced by an uneven-aged mosaic of late-successional tree species (Borman and Likens 1979, Oliver 1981).

Overview of the Study

I chose a watershed-scale approach for our examination of unmanaged landscapes. Although the exact definition of a watershed can vary (Allan 1995) the term "watershed-scale" is often used to describe catchments ranging in size from hundreds to thousands of hectares (Urban et al. 1987, Salwasser 1991). Using the term watershed-scale as opposed to the more generic "landscape scale" also emphasizes the characteristic physical structure of watersheds and its influence on vegetation patterns. A watershed can be viewed as a landscape characterized by a patchwork of forest stands that are linked by a network of stream channels (Figure 1.1, Swanson et al. 1997). This drainage system has the capacity to transport large amounts of wood, sediment, and water from hillslopes and low-order stream reaches into the high-order valleys (Gregory et al. 1991). Topographic variability within watersheds also influences the distribution of light, moisture, soil and other environmental factors across the landscape, as well as the initiation and movement of fires and other disturbances (Hack and

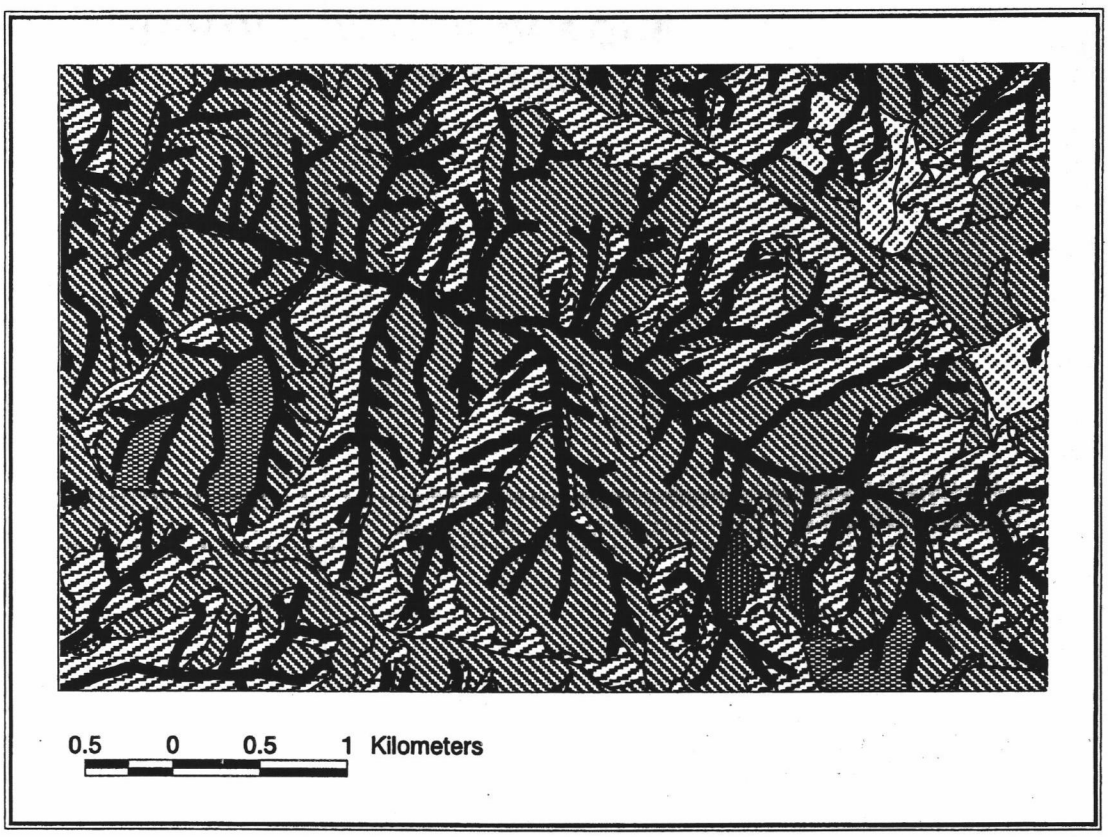


Figure 1.1: Conceptual model of watershed-scale vegetation patterns. Dark lines represent the riparian network. Various types of shading represent different patches of hillslope vegetation.

Goodlett 1960, Swanson et al. 1988, Agee 1993). These types of watershed processes are particularly strong in mountainous regions, where steep terrain emphasizes topographic gradients and increases the capacity for streams to transport material through the channel network. Because of the interconnected nature of aquatic and terrestrial watershed components, and because physiographic variability within watersheds creates a range of different habitats, the watershed-scale has emerged as an important framework for the conservation and management of both aquatic and terrestrial species (Naiman et al. 1992; 1997).

Studies of Pacific Northwest forests to date have not provided a comprehensive picture of vegetation pattern-process relationships at the watershed scale. Most forest vegetation research has concentrated either on the patchwork patterns of hillslope vegetation (Mladenoff et al. 1993, Spies et al. 1994, Frelich and Reich 1995) or on the longitudinal and latitudinal variation of riparian forests bordering the stream channels. (Andrus and Frehlich 1988, Bendix 1994, Minore and Weatherly 1994, Pabst and Spies 1998, Pabst and Spies in press). In addition, few studies have considered the full range of processes likely to influence vegetation in forested watersheds. Classical forest community studies have focused on the distribution of species along environmental gradients related to elevation and topography (Fonda and Bliss 1969, Zobel et al. 1976, DelMoral and Watson 1978), while many studies of forest change following disturbance have either not considered environmental variability, or controlled for it by comparing sites with a particular set of environmental characteristics (Henderson 1970, Spies and Franklin 1991, Acker et al. 1998). Many questions still remain as to how forest dynamics operate at a watershed scale. Do the disturbance regimes of riparian and hillslope forests operate independently, or are they linked by the propagation of large fires across the landscape? What roles do environmental gradients and disturbance patterns play in

shaping watershed vegetation patterns? Does vegetation response to these controlling factors differ in riparian areas compared to hillslopes?

I studied the 3,900 ha Cummins Creek Wilderness to address these questions and increase the amount of baseline information on forest pattern and dynamics in late-successional Coast Range watersheds. (Figure 1.2, Chapter 2). This 3,900 ha landscape encompasses one of the largest remaining blocks of uncut forest in the Oregon Coast Range, and provides a rare opportunity to study the relationships of vegetation patterns and processes in unmanaged watersheds. Our main goals in this study were to examine linkages between riparian and hillslope disturbance processes, to compare the structure and composition of riparian and hillslope forests, and to determine whether the major processes influencing vegetation patterns were different in these two portions of the watershed. The analysis was based on an intensive field survey in which I characterized forest vegetation, disturbance history, and environmental variables at a range of sites within the study area. These sites were also georeferenced using a global positioning system (GPS), which allowed me to link plot data with digital maps of terrain, streams, and vegetation in a geographic information system (GIS) for landscape analysis.

Knowledge about the structure and function of landscapes provides a basis for developing predictive models of vegetation patterns at a landscape scale. For example, complex, multilayered canopy structure is an important component of late-successional forest structure in the Pacific Northwest. In many areas of the Oregon Coast Range, however, multilayered canopy structure may develop slowly or not at all if shade-tolerant regeneration is not present to recruit into the overstory through canopy gap formation (Schrader 1998). Landscape-level maps of understory tree regeneration across a landscape would allow me to identify specific areas where the future development of late-successional structure might be

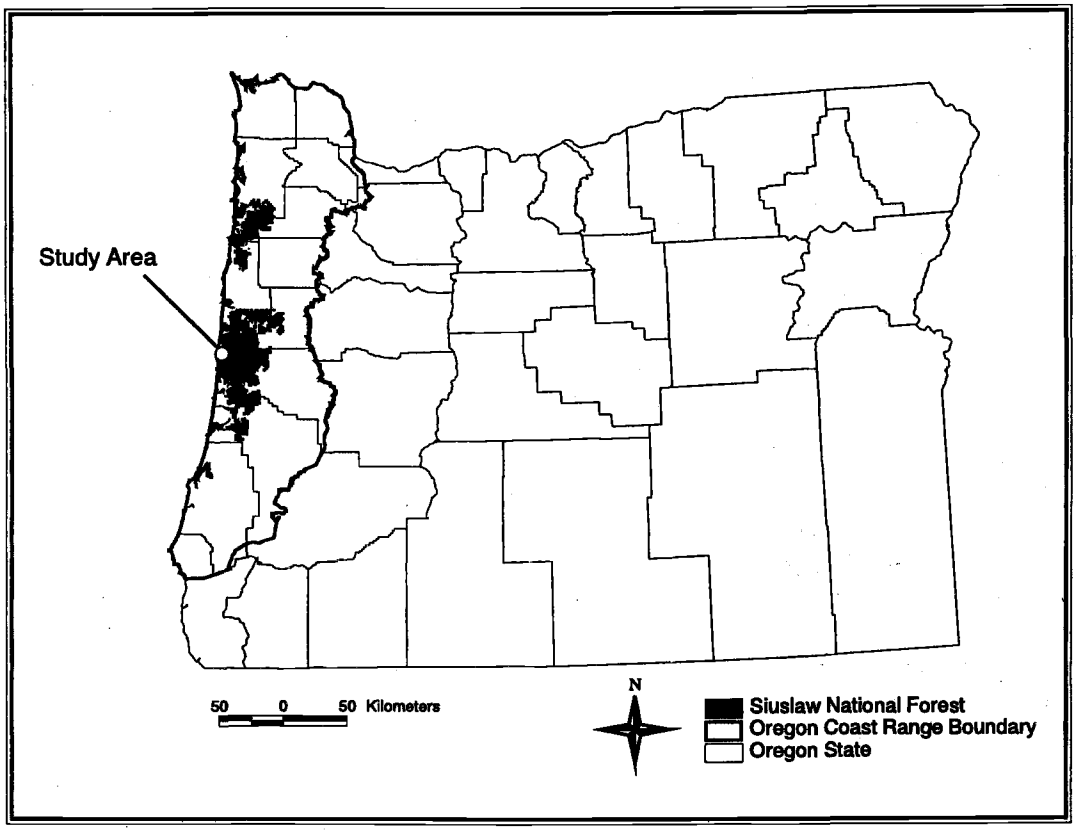


Figure 1.2: Location of the Cummins Creek Wilderness.

limited by a low abundance of shade-tolerant understory conifers. Understanding the ecological mechanisms that influence these patterns may also enhance our ability to model forest dynamics at the landscape scale.

This spatial information is currently unavailable because measurements of understory vegetation are taken in small field plots that are dispersed across the landscape. It may be possible to use a predictive vegetation mapping approach (Franklin 1995) to develop these types of maps. This method uses information about species-environment relationships, forest succession, and dispersal to predict vegetation patterns based on environmental variables derived from digital elevation models, overstory vegetation characteristics derived from aerial photographs and remote sensing, and riparian network characteristics obtained from stream maps. I applied the knowledge of vegetation patterns and watershed-scale processes gained in the first study to develop predictive maps of *T. heterophylla* and *P. sitchensis* advance regeneration for the Cummins Creek Wilderness (Chapter 3). My goals were to assess how much of the variation in understory regeneration could be explained using mapped predictor variables and determine the kinds of explanatory variables that were necessary to predict understory patterns.

Results from both the watershed-scale vegetation analysis (Chapter 2) and the predictive modeling exercise (Chapter 3) showed that amounts of *T. heterophylla* in the overstory and understory decreased with distance from remnant old-growth patches. Based on these results and other published data about the life history characteristics of this species, I hypothesized that the landscape distribution of *T. heterophylla* is partly related to seed source limitations that are linked to the spatial pattern of remnant old-growth patches. I also postulated that the sharp increase in fire frequency that occurred in the latter half of the 19th century (Weisberg 1998) could have led to high mortality of *T. heterophylla* across the

landscape and might account for the current patchy distribution of this species in the central Coast Range (Janet Ohmann, unpublished data). In order to further refine these hypotheses and assess the possible influences of disturbance and dispersal on the variability of *T. heterophylla* in time and space, I developed a simple, spatial simulation model (Chapter 4). I carried out a sensitivity analysis of the model to assess the sensitivity of *T. heterophylla* populations at the landscape scale to various disturbance and life-history parameters, and also examined population response to short-term increases in fire frequency.

CHAPTER 2

Assessing the Influences of Disturbance History and Environmental Variability on Forest Structure and Composition in Coastal Oregon Watersheds

Michael C. Wimberly and Thomas A. Spies

Abstract

Forested watersheds encompass an array of different physical environments, disturbance regimes, and biotic communities. More information about spatial and temporal forest patterns in unmanaged watersheds is needed to provide a foundation for management strategies aimed at conserving native biodiversity. We used tree age distributions and historical records to reconstruct recent fire history in the Cummins Creek Wilderness, located on the Oregon Coast. We also compared the species composition and structure of riparian and hillslope forests, and examined the relationships among vegetation patterns, environmental variability, and disturbance history. Most of the wilderness was affected by a catastrophic fire in the mid 19th century that burned both hillslope and riparian forests. Many areas reburned several times through the early 20th century, particularly the dry upper hillslopes. Riparian areas had high shrub cover, large proportions of overstory hardwoods, and high down wood volumes, while the conifer-dominated hillslopes hillslopes had high overstory density and basal area. Advance regeneration densities were higher in riparian forests within 5 km of the coast than in any other portion of our study area. Environmental constraints, seed dispersal limitations, and disturbance history all had a role in structuring the current landscape. Community composition on hillslopes and in riparian areas varied along a climatic gradient from moist maritime environments to dryer inland climates, but was relatively insensitive to forest age structure. The abundance of two fire-sensitive species, *Tsuga heterophylla* (western hemlock) and *Picea sitchensis* (Sitka spruce), decreased with distance from remnant old-growth patches, suggesting dispersal-limited recruitment following the historical fires. Fire history explained most of structural variability in hillslope forests. Older forests and forests with remnant trees had more structures characteristic of old growth, including large dominant trees, large snags, high volumes of down wood, and a diversity of tree sizes. Patterns of old-

growth structure in riparian forests were more related to distance form the coast than stand age. Conifer-dominated coastal riparian forests tending to have more old-growth features than hardwood-dominated inland forests. Forest management and restoration strategies that are narrowly based on a single ecological process will likely fail to produce the full range of habitat variability found in unmanaged watersheds.

Introduction

Understanding vegetation patterns and processes at the watershed scale is critical for maintaining biodiversity in forested landscapes. The physiographic structure of watersheds affects the distribution of solar radiation, moisture, and soil characteristics across the landscape (Swanson et al. 1988), and these physical patterns in turn influence the spatial pattern of biological communities within a watershed (Hack and Goodlett 1960). The distinctive structures of riparian and hillslope forests, for example, each provide habitat for different groups of plants, animals, and birds (McGarigal and McComb 1992, McComb et al. 1993, Pabst and Spies 1998). Riparian forests also provide critical linkages regulating the exchanges of wood, sediments, nutrients, and water between terrestrial and aquatic habitats (Gregory et al. 1991, Naiman et al. 1992). Movement of these materials through the drainage network connects various watershed components such that aquatic habitat in high-order streams is affected by forest conditions along low-order streams and on hillslopes (Benda 1990, Reeves et al. 1995). Given these considerations, it will be necessary to take the full range of habitats at the watershed scale into account when planning and managing for native biodiversity.

Human activities such as timber harvesting, agriculture, and urban development have significantly changed forest patterns in the Pacific Northwest since European settlement began

in the early 19th Century (Spies et al. 1994, Means et al. 1996, Ripple et al. in press). Decreasing amounts of older forest and increasing habitat fragmentation have led to concern for the viability of many native species. Recent management plans for federal lands have adopted watershed-level approaches to landscape analysis and restoration as key components of a regional forest management strategy (FEMAT 1993). These new management efforts currently are limited, however, by a lack of standards and guidelines to use for assessing the ecological integrity of watersheds. Vegetation research in unmanaged watersheds can help to address this problem by providing reference conditions against which to compare managed landscapes (Franklin 1987). We studied the 3,900 ha Cummins Creek Wilderness to increase the amount of baseline information on forest patterns in unmanaged Coast Range watersheds. We addressed several fundamental questions about watershed-scale forest dynamics. Do the disturbance regimes of riparian and hillslope forests operate independently, or are they linked by the propagation of large fires across the landscape? What roles do environmental gradients and disturbance patterns play in shaping watershed vegetation patterns? Do vegetation responses to these controlling factors differ in riparian areas compared to hillslopes?

Studies of forest communities have traditionally considered environmental variability to be the predominant factor influencing vegetation patterns. Environmental variables such as temperature, moisture, and solar radiation influence forest composition and structure by differentially affecting the regeneration, growth, and mortality of various species. These relationships have often been conceptualized as an overlapping series of realized niches arrayed along one or more environmental gradients (Whittaker 1967). Studies of forest vegetation in mountainous regions have emphasized the importance of elevation, which influences temperature and precipitation, and topography, which affects soil moisture and exposure to solar radiation, as the primary gradients controlling community patterns

(Whittaker 1956, Whittaker 1960, Peet 1981). Proximity to large bodies of water is another factor that can influence environmental and vegetation patterns (Vetaas 1992). Although precipitation increases with distance from the coast as air masses are lifted over the Coast Range (Hemstrom and Logan 1986), moisture stress can actually be lower near the coast because of cool summer temperatures and the prevalence of coastal fog (Franklin and Dyrness 1988). Riparian environments tend to be cooler and moister than the surrounding hillslopes because of topographic shading, drainage from adjacent hillslopes, and movement of surface water through the hyporheic zone (Naiman et al. 1992).

Natural disturbances also play a major role in shaping forested landscapes (Oliver and Larson 1990). Catastrophic disturbances such as fires, floods, insect outbreaks, and large-scale windthrow kill large patches of trees and create a mosaic of forest age classes. The distribution of these age classes is an important component of forest pattern because both species composition (Connell and Slatyer 1977, Franklin and Hemstrom 1981) and forest structure (Oliver 1981, Peet and Christenson 1987) change over time following stand-replacing disturbance. The particular species that occupy a site following disturbance may depend on the specific agent causing the disturbance (Oliver et al. 1985), the size of the forest opening created by the disturbance (Gray and Spies 1996), or seed availability in the disturbed area (Reader et al. 1995). Minor disturbances such as low-intensity fires, localized windthrow, and endemic diseases that kill only a portion of the trees in a stand can also cause structural and compositional changes. Depending on their nature and magnitude, these partial disturbances may retard, accelerate, or completely change the forest's successional trajectory (Oliver and Larson 1990, Weisberg 1998).

Although disturbances are largely unpredictable, some aspects of disturbance regimes are related to physical landscape features. The temporal and spatial pattern of fires, for

example, varies with climate and topography. Fires in cool, moist environments tend to occur infrequently, but are often larger and more severe than the more frequent, patchy fires that burn in warm and dry environments (Morrison and Swanson 1990). Firebreaks formed by ridgelines and unvegetated areas can limit the spread and influence the shape and size of fires (Hemstrom and Franklin 1982). Windthrow may be more likely to occur on shallow soils or slopes exposed to prevailing winds (Ruth and Yoder 1953, Sinton 1996). Disturbances unique to riparian areas such as floods and debris flows are confined to the channel network, and mostly affect trees on valley floor landforms (Sigafoos 1961, Yanosky 1982, Swanson et al. 1998). The effects of disturbance resulting from a particular flood vary throughout the stream network with changes in channel gradient and the degree to which the channel is constrained by surrounding hillslopes (Hupp 1982, Grant and Swanson 1995).

Most forest vegetation studies in the Pacific Northwest have focused either on temporal vegetation change following disturbance or on the relationship between community composition and the environment. Forest community studies have often de-emphasized the impact of disturbance by sampling only undisturbed old-growth vegetation (Fonda and Bliss 1969, Zobel et al. 1976, DelMoral and Watson 1978). Conversely, many studies of forest change following disturbance have either not considered environmental variability, or controlled for it by comparing sites with a particular set of environmental characteristics (Henderson 1970, Spies and Franklin 1991, Acker et al. 1998). Only a few studies have explicitly compared the effects of both environment and disturbance on forest patterns. For example, Ohmann and Spies (1998) found that time since disturbance had a weak correlation with woody plant community composition at the provincial and regional scales. In contrast, Weisberg (1998) found that forest structure exhibited strong relationships with both disturbance history and physiographic setting in a 45,000 ha landscape in the Central Oregon

Cascades. No studies to date, however, have examined the interrelationships of vegetation, environment, and disturbance at a watershed scale.

Our overarching hypothesis was that both environment and disturbance have played significant roles in structuring the current vegetation patterns in the Cummins Creek Wilderness, but have had different effects in riparian areas as opposed to hillslopes. We addressed several general working hypotheses.

Hypothesis 1: Disturbance regimes differ in riparian areas compared to hillslopes

We hypothesized that riparian areas would experience unique disturbances such as floods and debris flows as well as wind, disease, and other disturbances that commonly occur on hillslopes (Gregory et al. 1991). We also hypothesized that fires were more patchy and less severe in the moist riparian areas than on the warmer, drier hillslopes, leaving more old-growth remnants in the riparian forests (Agee 1988). We expected the hillslopes, in comparison, to be composed mainly of younger, single-cohort stands that established after high-severity burns.

Hypothesis 2: Riparian forests have distinctive structure and composition compared to hillslope forests.

We hypothesized that the differences in environment and disturbance regime between riparian and upland sites would lead to different forest structures and woody plant communities. Hardwoods and shrubs, particularly *Alnus rubra* (red alder) and *Rubus spectabilis* (salmonberry), thrive in the moist, frequently disturbed riparian environments (Carlton 1988), and we expected to find high levels of hardwoods and shrubs in riparian forests (McGarigal and McComb 1992, Hayes et al. 1996, Pabst and Spies in press). We hypothesized that intense shrub competition and lack of conifer seed sources would limit tree regeneration in riparian areas (Minore and Weatherly 1994, Hibbs and Giordano 1996, Pabst

and Spies In press), and that regeneration densities would therefore be higher on hillslopes. We expected that overstory density and basal area would be lower in riparian areas than on hillslopes because of low tree regeneration combined with high mortality from frequent fluvial disturbances (Sigafoos 1961, Yanosky 1982, Swanson et al. 1998).

Hypothesis 3: Disturbance history is the primary factor explaining structural gradients, while environmental variability is the main factor influencing community gradients.

Principles of stand dynamics (Oliver and Larson 1990) emphasize the affects of disturbance on forest structure. Many types of forests pass through a series of structural stages following a stand-replacing disturbance (Oliver 1981). Minor disturbances such as windthrow and low-intensity fires can also affect forest structure by creating gaps in the forest overstory, creating snags and down logs, and initiating new cohorts of trees in the understory. Species composition also changes with time since disturbance, but we expected these changes to be relatively minor given the long life-spans of Pacific Northwest conifers and the relatively slow process of succession in these forests (Franklin and Hemstrom 1981). Many tree and shrub species are present throughout all phases of stand development in Pacific Northwest forests, although subtle shifts in community composition do occur over time (Schoonmaker and McKee 1988, Halpern and Spies 1995). We hypothesized that species composition would instead be related primarily to environmental variation controlled by physiographic gradients (Whittaker 1967). We expected the dominant gradients to encompass climatic change from the cool, wet Pacific coast to warmer and drier inland areas, and topographic variation in soil moisture from the moist lower hillslopes and riparian areas to dry sites along the ridges.

Hypothesis 4: Vegetation patterns on hillslopes areas are primarily linked to environmental factors, while vegetation patterns on hillslopes have a stronger relationship with disturbance history.

We hypothesized that hillslope sites would span a wide range of environmental conditions because soil properties, moisture availability, and exposure to solar radiation vary with slope position, slope angle, and aspect (Swanson et al. 1988). We expected that these strong physiographic gradients would explain a large proportion of the variability in hillslope vegetation. In contrast, we hypothesized that riparian areas would be all relatively cool and moist, with less environmental variability as a function of physical gradients. We hypothesized that riparian vegetation would have a stronger relationship with disturbance history than environmental variability, given the heterogeneous mix of disturbances we expected would occur in riparian areas (Gregory et al. 1991). We also postulated that some of these disturbance patterns would be correlated with physical variables such as valley floor width, channel gradient, and position in the drainage network (Hupp 1982, Baker 1989, Grant and Swanson 1995).

Study Area

The Cummins Creek Wilderness, located on the Oregon Coast 10 km south of Yachats, encompasses nearly 4,000 ha and includes the majority of the Cummins Creek, Little Cummins Creek, and Bob Creek watersheds (Figure 2.1). The main stems of these watersheds flow in an east to west direction, emptying directly into the Pacific Ocean. This area is mostly underlain by Yachats basalt, rather than the Tyee sandstone that dominates most of the central Coast Range. Differential weathering has produced deeply dissected terrain with long steep

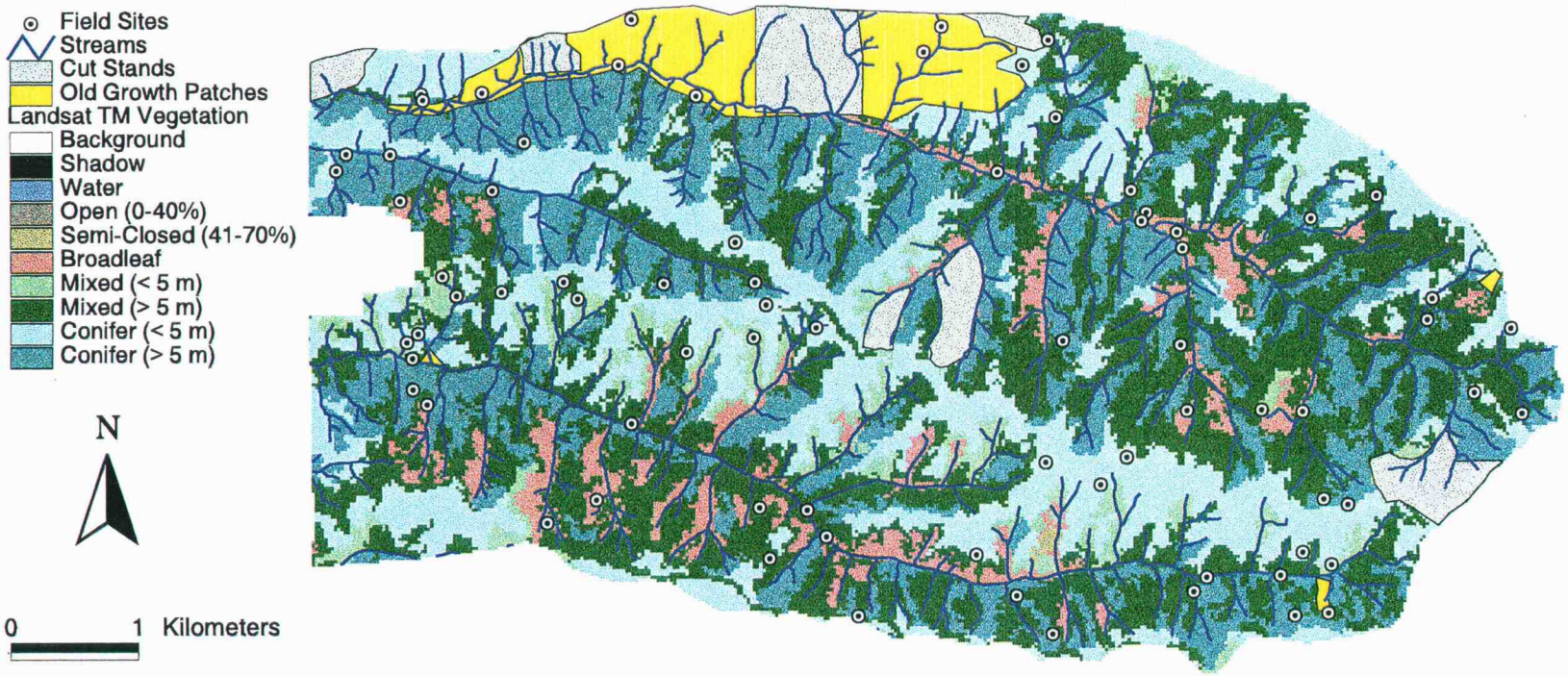


Figure 2.1: Map of overstory vegetation and field site locations in the Cummins Creek Wilderness. Overstory vegetation is derived from a 1988 Landsat TM image, and is classified by percent canopy closure, hardwood/conifer composition, and conifer crown diameter. Areas with previous management activity were not sampled.

streams. Soils are mostly well drained Andisols and Inceptisols, and the wide valley floors of Cummins and Bob Creeks are composed mainly of alluvial sediments.

The study area falls mostly within the Sitka spruce zone (Franklin and Dyrness 1988) with its eastern portion transitioning into the western hemlock zone. As a whole, the area experiences the maritime climate typical of the Pacific Northwest. Winters are mild and wet while summers are relatively cool and dry, with less than 80% of the annual precipitation falling during the growing season (Lassoie et al. 1985). Low-lying fog is common near the coast, and may extend several kilometers inland along river valleys (Franklin and Dyrness 1988). Common tree species include *Picea sitchensis* (Sitka spruce), *Tsuga heterophylla* (western hemlock), *Pseudotsuga menziesi* (Douglas-fir) and *Alnus rubra* (red alder). *Thuja plicata* (western redcedar) and *Acer macrophyllum* (bigleaf maple) are less common.

The Cummins Creek wilderness was burned by catastrophic wildfires during the late 19th and early 20th centuries, creating a mosaic of young stands and patches of old-growth forest remnants. Frequent floods have produced a finer-scale patchwork of conifers and hardwoods on the valley floors. Windthrow is common along the ridges, although large blowdown patches are rare. Both insects (bark beetle and spruce tip weevil) and disease (root rot and hemlock mistletoe) are present in the study area, but they are not believed to have a major impact on these forests (Siuslaw National Forest 1995). Less than 5% of the study area has been cut, mostly around its perimeters, and these harvested areas were excluded from the present study.

Methods

Vegetation Data

We collected data from 72 field sites during the summer of 1997 using a stratified random sampling design (Figure 2.1). We divided the landscape into two geographic zones (< 5 km from the coast and > 5 km from the coast) and five topographic zones (high-order riparian areas, low-order riparian areas, lower hillslopes, middle hillslopes, and upper hillslopes). Hillslopes were then further subdivided into two aspect zones (north and south aspects). We created a map of these zones using a GIS (geographic information system) and randomly selected 4 sites in each of 12 hillslope strata (2 geographic zones x 3 topographic zones x 2 aspect zones) and 6 sites in each of 4 riparian strata (2 geographic zones x 2 topographic zones). Because stands containing trees that established before 1800 were uncommon in our study area, only five of the randomly selected sites fell within these old-growth patches. To increase the number of old-growth sites in our sample, we sampled three additional sites located within old-growth patches during the summer of 1998. These sites were randomly selected using an old-growth map derived from aerial photographs (Figure 2.1).

We located the randomly selected sites in the field using topographic and vegetation maps. After finding the approximate location of each hillslope site, we established the center at a random distance and offset to reduce observer bias in site selection. We established the center of each riparian site on the valley floor at a random location between the stream channel and the constraining footslope. Valley floors were typically narrow in the first and second order streams (< 10 m in width) so the low-order riparian sites mostly encompassed the adjacent footslopes. Most of the high-order riparian sites were located entirely on the

broad valley floors of the third and fourth order streams (20 – 140 meters in width), although some also overlapped the adjacent footslope.

Each sample site encompassed an area of approximately 0.25 ha, and included three systematically located sets of nested circular plots. We measured live trees (≥ 5 cm dbh) and snags (≥ 10 cm dbh and > 2 m height) in 333 m^2 plots. We recorded diameter at breast height (dbh) and species of live trees and dbh of snags. Each live tree was also classified as either overstory (<50 % of crown length beneath the level of the main canopy) or understory (≥ 50% of crown length beneath the level of the main canopy). We tallied seedlings (≥ 10 cm height and < 1 m height) and saplings (≥ 1 m height and < 5 cm dbh) by species in 167 m^2 plots. We estimated percent shrub cover by species in 20 m^2 plots using eight cover classes based on an arc sine–square root transformation of percent cover (Muir and McCune 1987). Within each set of plots, we measured down wood volume along a 20 m transect using the line intercept method. We measured percent high shrub cover (≥ 1.5 m height) at three points along each transect using a moosehorn (Mueller-Dombois and Ellenberg 1974). Plot measurements were slope-corrected and then aggregated to the site level.

The centers of all sample sites were georeferenced using a Trimble Pathfinder Pro XR Global Positioning System (GPS). A minimum of 25 3-dimensional position fixes was obtained for each sample site. Position fixes were taken with a minimum satellite elevation angle of 15 degrees, minimum signal to noise ratio of six, and a maximum PDOP (position dilution of precision) of six. Site locations were differentially corrected using data from the United States Forest Service base station in Portland, OR.

Environmental Data

We took field measurements of slope at each sample site. On hillslopes sites slope was measured along the steepest line of descent, while in riparian areas slope was measured as the channel gradient. We also measured valley floor width in riparian areas as the total distance between constraining footslopes, taken perpendicular to the stream. We computed additional environmental variables in a Geographic Information System (GIS). The GPS locations of sample sites were converted into a GIS point data layer, and the site locations were then overlaid on a U.S. Geological Survey 30 m digital elevation model (DEM). Elevation was obtained directly from the DEM. We computed a slope curvature index in Arc/Info Grid to distinguish convex landforms (high index values) from concave landforms (low index values). Slope position was computed using an algorithm that interpolated between valley bottoms and ridges – values ranged from 0 (valley bottoms) to 100 (ridgetops). Total solar radiation input during the growing season (May-September) was calculated using the SolarImg program (Harmon and Marks 1995). Weather data used to parameterize this model were taken from the nearest weather station in Newport, Oregon. Topographic moisture index (Beven and Kirkby 1979) was calculated as a function of drainage area and slope. Soil transmissivity was not included in this computation as reliable values were not available for the entire watershed. We also used the digital elevation model to determine the approximate location of the coastline and computed distance from each site to the coastline in Arc/Info Grid. We used a detailed stream layer provided by the Siuslaw National Forest to classify streams by stream order (Strahler 1952). Distance to each site from the nearest stream was computed in Arc/Info Grid.

Disturbance Data

Our goals in sampling tree ages was to identify the time since the last stand-replacing disturbance occurred at each site, and to determine whether any additional, minor disturbances had occurred since that time. We obtained increment cores at breast height from at least three overstory shade-intolerant trees at each site. *P. menziesii* and *P. sitchensis* were preferentially selected, although *T. heterophylla* and *T. plicata* were cored at a few locations where they were the only dominant conifers present. We first cored the largest shade-intolerant conifer at each site, and then cored at least two smaller conifers selected to span the range of dominant tree sizes. At sites that appeared to have experienced a second low-severity fire we cored at least two trees from each suspected cohort. We also obtained two to four red alder cores at sites where alder was present.

We mounted and sanded all the core samples and determined tree ages at breast height by counting annual rings under a dissecting microscope. When cores bypassed the pith we estimated tree age by extrapolating to the estimated pith based on the curvature of the annual rings. Twenty-five percent of the trees we cored were larger in radius than the length of our longest increment borer (42 cm). In these cases we calculated distance to the pith as the difference between core length and tree radius, and estimated the number of years to the pith based on the width of the oldest 5-10 annual rings on the core. Because trees were cored at breast height, ages represent the time since breast-height recruitment rather than seedling establishment. The time required to reach breast height probably varied depending on environmental conditions and the amount of competing vegetation at each site. Using breast-height cores from trees that established after clearcuts of known ages, we estimated that conifers generally required between five and fifteen years to reach breast height.

All sites, including those with old-growth remnants, had evidence of burning after 1850. Stand age was assumed to be the age of the oldest tree at each site that had established after 1850. Trees established before 1850 were not incorporated into the stand age determination because we could not reliably determine the ages of these trees, and because they would have created outliers in the stand age distribution. Instead, we used an indicator variable to classify sites with old-growth remnants (trees > 200 years old). We classified sites as having multiple cohorts if there was evidence that the stand-initiating fire was followed by a second, low-severity fire that led to the establishment of another cohort. The younger cohorts in these stands typically established 20-30 years after the older trees, and the older trees often had scars on their uphill sides that we interpreted as fire scars. Trees in the younger cohorts were densely spaced with small lower branch stubs; we interpreted these structural characteristics as evidence that the younger trees had established rapidly following a disturbance rather than gradually invading an open area.

We created a map of remnant old-growth patches using 1995 color aerial photographs with a scale of 1: 12,000 viewed through a mirror stereoscope. Areas were classified as old-growth patches if they were estimated to have three or more remnant trees per hectare. Individual remnant trees were not mapped because they could not be accurately identified using the aerial photographs. Old-growth patch boundaries were delimited using acetate overlays on 1:25,000 scale orthophotos. These boundaries were verified in the field at several locations. The patch maps were digitized and converted to 30 m raster data layers, and the distance of each site from the nearest old-growth patch was computed using Arc/Info Grid.

We categorized stands as having recent wind disturbance if one or more trees had been either snapped or uprooted in the southwest-to-northeast direction of the prevailing winter winds. We classified sites as having mass movement disturbance if we found evidence

of recent landslides, slumps, or debris flows. We characterized riparian sites as having flood disturbance if they had evidence of significant scour or deposition from recent floods, or if they had linear patches of streamside alder that were inferred to have established from previous floods. We classified stands as diseased if we found evidence of overstory tree mortality insects or disease. Diseases known to be present within the study area included *Fomes annosus* (annosus root rot), *Phellinus weirii* (laminated root rot), and *Arceuthobium tsugense* (hemlock dwarf mistletoe) (Siuslaw National Forest 1995). No major insect outbreaks have been reported within the study area, but insects such as *Dendroctonus pseudotsugae* (Douglas-fir beetle), *Dendroctonus rufipennis* (spruce beetle) and *Pissodes sitchensis* (spruce tip weevil) often occur in coastal forests.

Data Analyses

We generated histograms of tree ages at different topographic positions to describe temporal patterns of overstory regeneration, and to explore their relationships with landscape position. We compared these age-class distributions with accounts of historical fires obtained from independent sources, taking into account the time lag between disturbance and breast-height recruitment. These sources included reports based on historical records (Morris 1934) dendroecological reconstruction (Impara 1997) and cadastral land survey records from the late 19th century (Dewberry 1994). We also examined maps and written accounts of land surveys that were conducted between 1910 and 1920 to assess the agricultural suitability of lands claimed under the Forest Homestead Act of 1906. These surveys provided information about historical human land use in and around the present day Cummins Creek Wilderness, as well as descriptions of early 20th century vegetation patterns.

We summarized species composition at each site by computing basal area per hectare for each of the six major tree species and mean cover index for each of the eleven shrub species found in our samples. We also computed twelve additional variables describing various aspects of forest structure. Structure variables included total basal area, total tree density, large tree (> 100 cm dbh) density, understory tree density, mean dbh, large (> 50 cm dbh) snag density, standard deviation of dbh and down wood volume. These variables were selected because previous research has shown that they reflect temporal changes associated with the development of old-growth forest structure (Spies and Franklin 1991). We also included percent hardwood basal area, percent high (> 1.5 m) shrub cover, percent shade-tolerant basal area, and advance regeneration density (total of seedling plus sapling densities) to describe other important aspects of structural variability in Coast Range forests.

We tested the null hypotheses that mean values of stand age, forest structure, and species abundance variables were similar in riparian areas and on hillslopes using two-sample *t*-tests (Zar 1984). Where necessary, we transformed the variables using either root or logarithmic transformations. We examined advance regeneration patterns in greater depth by comparing the density and species composition of seedlings and sapling in coastal (< 5 km from the coast) versus inland (> 5 km from the coast) forests. We tested the null hypothesis that the proportion of sites falling into each disturbance class (old-growth remnants, multiple cohorts, mass movement, wind, disease, and flooding) was similar in riparian areas and on hillslopes using Fisher's exact test (Zar 1984).

We used forward stepwise regression models to examine associations between disturbance variables and environmental variables. We fit two separate models for each disturbance variable: one for the hillslope sites and one for the riparian sites. We use multiple linear regression to model the continuous disturbance variables (stand age and distance from

old growth). Independent variables were added to the regression models in order of decreasing error sum of squares reduction with $p < 0.05$ required for variables to enter based on a partial F-test (Neter et al. 1989). We used multiple logistic regression to model the binary (presence/absence) disturbance variables. Independent variables were added to the regression models in order of decreasing reduction in deviance with $p < 0.05$ required for variables to enter based on a Chi-squared test of the drop in deviance (Ramsey and Shafer 1997).

We used RDA (redundancy analysis) on a correlation matrix to carry out direct gradient analyses of species composition and forest structure as a function of environmental and disturbance variables. RDA is a constrained ordination technique based on a linear response model (TerBraak and Prentice 1988). We decided to use direct rather than indirect ordination because our objective was to explore hypotheses about the relationship between vegetation and particular sets of explanatory variables (Okland 1996). We recognize that linear methods have been criticized as inappropriate for many types of ecological ordination (Beals 1984). Exploratory analysis of our data sets, however, revealed that both structural and compositional gradients were fairly short, and exhibited linear rather than unimodal relationships with individual structural and species variables. In this case RDA is more appropriate than CCA (canonical correspondence analysis), an alternative direct gradient analysis method that uses a unimodal response model (TerBraak and Prentice 1988).

We computed separate ordinations for forest structure and species composition, and for hillslopes and riparian areas. Vegetation variables were transformed using root and logarithmic transformation where necessary to enhance multivariate normality and decrease the influence of outliers. We used a forward stepwise method to select variables for each ordination with independent variables added in decreasing order of the total variance explained. We tested each independent variable's relationship with the vegetation variables

against a null hypothesis of random association using a permutation test (terBraak and Smilauer 1998). Only independent variables with p-values < 0.05 were allowed to enter the final model. We also used permutation tests to test the null hypothesis that the amount of variation explained by each ordination axis was no greater than would be expected under randomization (terBraak and Smilauer 1998). We described the first two axes of each ordination using biplots of vegetation variables along with the environmental and disturbance variables selected by the stepwise routine (TerBraak 1994). We also examined the correlation of ordination axes with environmental and disturbance variables not selected in the stepwise routine, because these variables can still be useful in interpreting the ordination axes.

We used variation partitioning methods to determine the portion of the total variation explained by each ordination that was attributable to disturbance variables alone, environmental variables alone, and to the synergistic effects of environment and disturbance (Borcard et al. 1992, Okland and Eilertsen 1994). To partition the variation of a particular set of response variables, we first performed separate stepwise RDAs to determine the percentage of total variation explained by environmental variables (E), and by disturbance variables (D). We then used partial RDA with environmental variables as the explanatory variables and disturbance variables as covariates to determine the amount of variation attributable to the environmental variables independent of any correlation with disturbance (E|D). We applied the following formulas to compute the percentage of variance explained by each category.

TVE (Total Variation Explained) = D + E|D

Variation explained by environmental variables, independent of disturbance = E|D

Variation explained by disturbance variables correlated with environmental variables = E – E|D

Variation explained disturbance variables, independent of environment = D + E|D – E

We carried out this variation partitioning for each of our four ordinations: species composition on hillslopes; species composition in riparian areas; forest structure on hillslopes; and forest structure in riparian areas. Absolute estimates of TVE derived from constrained ordinations are not strictly comparable among different data sets (Ohmann and Spies 1998, Okland 1999). We instead expressed each category as a percentage of TVE and compared these percentages between riparian and hillslope ordinations, and between species composition and forest structure ordinations.

Results

Disturbance History

Several historically recorded fire events occurred in the vicinity of the Cummins Creek Wilderness. Between 1849 and 1952 one or more large fires burned approximately 325,000 hectares between the Siuslaw and Siletz rivers (Morris 1934). In 1868 fires were reported near Yaqunia bay, 35 km north of Cummins Creek. Dendroecological evidence from a previous study indicated that fires occurring at both of these dates burned within 5 km of our study area (Impara 1997). 1902 was also a year of widespread fire in the Pacific Northwest, with Coast Range fires reported at Newport, Tillamook, Mapleton, and Mary's Peak (Morris 1934). In 1910, a fire occurred on Fairview Mountain 10 km south of Cummins Creek (Bogue and Yunker 1991). Early 20th century survey maps of the western boundary of the Cummins Creek wilderness also list some ridges as "burned in 1910".

Landscape age-structure analysis revealed a large gap in the age class distribution between trees that established before 1800 and trees that established after 1850 (Figure 2.2). The reinitiation of overstory tree recruitment after 1850 suggested that the study area burned in the 1849 fire. This conjecture was supported by the observations of surveyors in the late

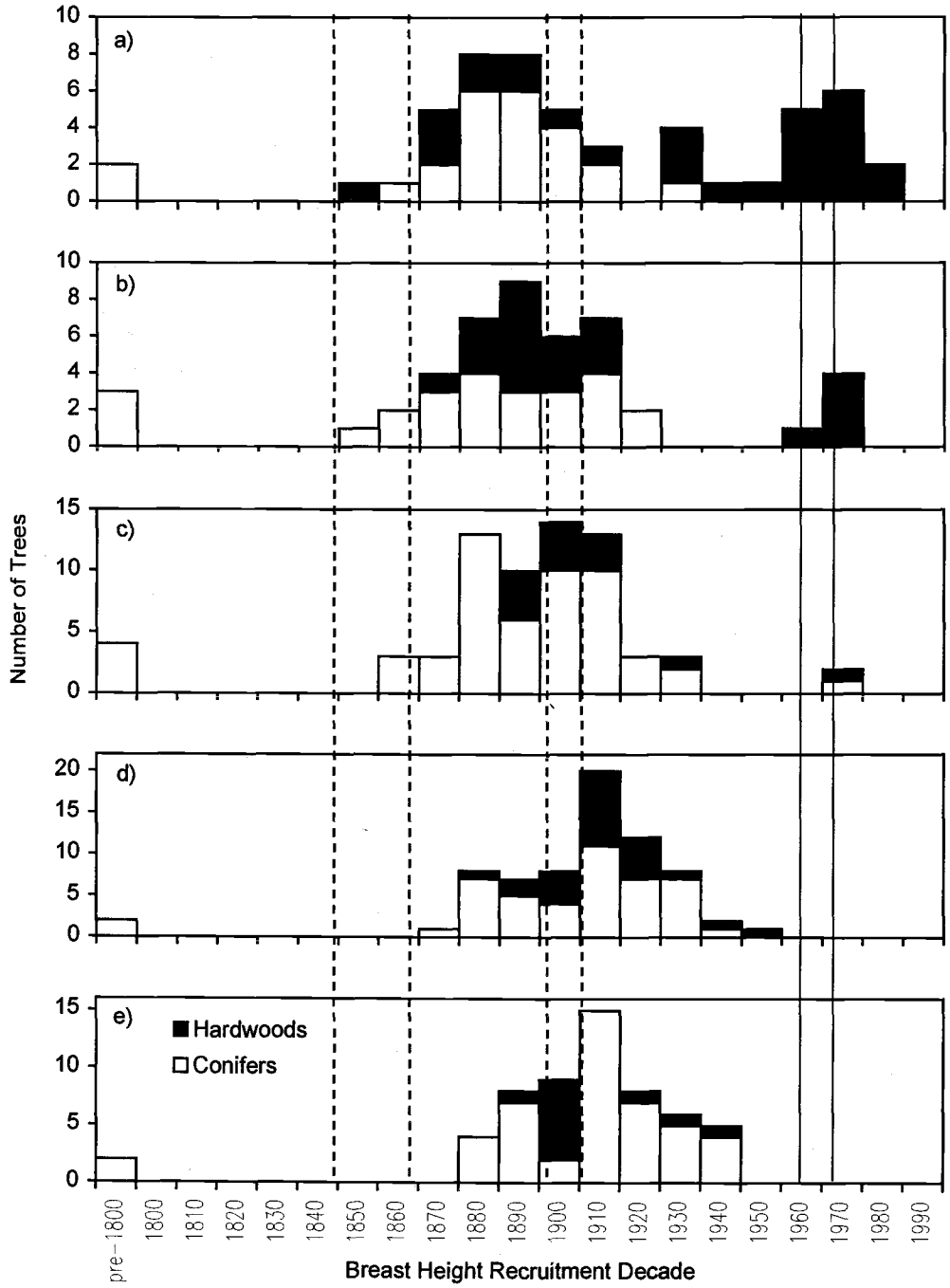


Figure 2.2: Age class distribution by topographic position. a) high-order riparian areas, b) low-order riparian areas, c) lower hillslopes, d) middle hillslopes and e) upper hillslopes. Individual bars represent the total number of trees sampled within each age class at each topographic position. Dashed lines denote historical fire years in 1849, 1868, 1902, and 1910. Solid lines represent recent flood years in 1964 (100-year flood) and 1973 (50-year flood).

19th century, who reported dense shrub thickets over most of the study area and supposed that a large fire had occurred forty to fifty years in the past (Dewberry 1994). We found large remnant snags, stumps, and logs at 58% of our sample sites, suggesting that late-successional conifer forests covered much of the landscape prior to 1850. In riparian areas and on lower hillslopes, breast height recruitment did not peak until after 1880 (Figure 2.2a-c). Overstory recruitment was delayed even longer on middle and upper hillslopes, peaking between 1911 and 1920 (Figure 2.2d-e). These delays could have been caused by seed source limitations following the catastrophic 1849 disturbance, competition from shrubs, or reburns in the late 19th and early 20th centuries.

Several lines of evidence supported the hypothesis of multiple reburns in the study area, particularly on the upper hillslopes. First, the peaks in overstory recruitment (after 1880 in riparian areas and on lower hillslopes, and after 1910 and middle and upper hillslopes), followed historical fire periods in the Coast Range (1868 and 1902-1910). We also found direct field evidence of a reburn. The corner of sections 20, 21, 28, and 29 in T15S R12W was initially surveyed sometime between 1879 and 1892, and listed as having live Douglas-fir and alder greater than 6" in diameter (Dewberry 1994). The forest around this section corner is currently a dense *P. menziesii* stand with no trees greater than 70 years old at breast height, indicating that a fire sometime between 1892 and 1910 destroyed the previous witness trees. In addition, survey notes from Forest Homestead Act applications mention multiple fires. In 1915, one surveyor describing a potential homestead site in the southwest portion of our study area noted that: "These ridges have burned over numerous times, which has killed nearly all young timber growth, so that now practically all there is left is brush of different kinds and alder coming along in the canyon bottoms."

Overstory recruitment in high-order riparian areas increased between 1931 and 1940, and again between 1961 and 1980 (Figure 2.2a-b). The younger hardwoods were all *A. rubra*, and were found on low floodplains close to the streams. Most of these trees had established after one of two recent floods: a 100-year flood in 1964 and a 50-year flood in 1973 (Siuslaw National Forest 1995). Trees in these age classes were found at several high-order sites in both the Cummins Creek and Bob Creek basins. The young hardwoods in the low order riparian areas were all found at one site that had a relatively wide, low gradient valley floor, and was just above the junction with Cummins Creek. Deposits on the Cummins Creek valley floor indicated that one or more debris flows had occurred in the tributary channel and initiated the *A. rubra* cohort. Although young *A. rubra* were not found at any of our other low-order riparian sites, we did note that several steep, first and second order streams we did not sample had linear patches of small alder, suggesting recent debris flow disturbance. The two young trees found on lower hillslopes (Figure 2.2c) both occurred at the same site, and were associated with a small landslide that may have been linked to one of the previously mentioned flood events.

Differences Between Riparian and Hillslope Forests.

Mean stand age was higher in riparian areas than on hillslopes (Table 2.1). Sites with old-growth remnant trees were rare both in riparian areas and on hillslopes, as were sites with multiple cohorts (Table 2.2). Evidence of flooding was found in just over half of the riparian areas. Mass movement occurred more frequently in riparian areas than on hillslopes, while windthrow was more common on hillslopes than in riparian areas. We did not find evidence of overstory mortality that was directly attributable to insects or disease at any of our sites. Several sites were infected with hemlock dwarf mistletoe, which had caused deformation in

Table 2.1: Mean values (with standard errors in parentheses) of stand age, stand structure variables, tree species basal area, and shrub species cover for hillslope and riparian areas. All variables are expressed on a per-hectare basis. *P*-values are from two-sample *t*-tests.

	Hillslope	Riparian	p-value
Stand Age	101.7 (2.9)	115.9 (2.8)	0.003
Stand Structure			
Basal Area (m^2)	72.4 (4.3)	38.9 (5.6)	< 0.001
Overstory Tree Density	281.4 (18.5)	158.8 (21.0)	< 0.001
Large (> 100 cm dbh) Tree Density	18.4 (3.0)	12.9 (2.8)	0.473
Understory Tree Density	52.0 (8.4)	37.9 (12.5)	0.319
Regeneration Density	301.2 (104.9)	1445.0 (410.9)	0.005
Mean dbh (cm)	51.9 (1.8)	46.0 (2.9)	0.075
Std. Dev. of dbh (cm)	27.5 (1.5)	31.3 (2.7)	0.193
Large (> 50 cm dbh) Snag Density	8.7 (1.5)	6.9 (1.9)	0.605
Down Wood Volume (m^3)	704.0 (125.2)	1837.8 (236.0)	< 0.001
Percent High Shrub Cover	13.3 (2.4)	27.9 (4.9)	0.003
Percent Shade Tolerant Basal Area	0.11 (0.02)	0.17 (0.04)	0.144
Percent Hardwood Basal Area	0.13 (0.03)	0.34 (0.07)	< 0.001
Tree Species Basal Area (m^2)			
Acer macrophyllum	0.5 (0.3)	4.1 (2.1)	0.024
Alnus rubra	5.3 (1.1)	5.4 (1.0)	0.268
Picea sitchensis	8.6 (2.8)	15.6 (5.3)	0.108
Pseudostuga menziesii	49.2 (4.8)	6.1 (2.0)	< 0.001
Thuja plicata	1.6 (0.9)	1.0 (0.5)	0.874
Tsuga heterophylla	7.2 (1.7)	6.7 (2.5)	0.984
Shrub Species Cover (mean cover class)			
Acer circinatum	0.5 (0.2)	0.8 (0.3)	0.378
Berberis nervosa	1.1 (0.2)	0.3 (0.2)	0.009
Gaultheria shallon	1.7 (0.2)	0.8 (0.2)	0.014
Menziesia ferrungia	0.4 (0.1)	1.0 (0.2)	0.002
Ribes bracteosum	0.02 (0.02)	0.9 (0.2)	< 0.001
Rubus parviflorus	0.4 (0.1)	0.2 (0.01)	0.235
Rubus spectabilis	1.8 (0.2)	3.2 (0.3)	< 0.001
Rubus ursinus	0.5 (0.1)	0.08 (0.1)	0.015
Sambucus racemosa	0.6 (0.1)	1.0 (0.2)	0.072
Vaccinium ovatum	0.6 (0.2)	0.6 (0.2)	0.993
Vaccinium parvifolium	1.8 (0.1)	1.5 (0.2)	0.247

Table 2.2: Percent of hillslope and riparian sites falling within each disturbance category. *P*-values are from Fisher's exact test.

	Hillslope	Riparian	p-value
Remnant trees	9.8%	12.5%	0.701
Multiple cohorts	15.7%	12.5%	1.000
Flooding	0%	54.2%	< 0.001
Windthrow	23.5%	4.2%	0.050
Mass movement	5.9%	33.3%	0.004

Table 2.3: Regression models of disturbance variables as a function of physiographic variables at riparian and hillslope sites. Linear regression models were used to predict stand age and distance from old growth, while logistic regression models were used to predict categorical disturbance variables. Variables were selected using a forward stepwise procedure with $p < 0.05$ required to enter. R^2 for logistic regression equations was computed using the method of Nagelkerke (1991).

	Regression Equation	R^2
Hillslopes		
Stand age (years)	stand age = 85.561 + 0.332 (slope) + 0.00397 (distance from coast) - 0.0634 (elevation)	0.30
Distance from old growth (m)	sqrt(distance from old growth) = 27.059 + 8.016 (slope curvature)	0.10
Riparian Areas		
Distance from old growth (m)	sqrt(distance from old growth) = 13.681 + 0.00263 (distance from coast)	0.17
Flooding	logit(flood) = - 3.097 - 2.640 (slope curvature)	0.52
Mass movement	logit(mass movement) = 3.107 – 1.666 (stream order)	0.49

T. heterophylla but did not kill the trees outright. We also noticed several isolated patches of dead, overstory *P. menziesii* that appeared to be caused by laminated root rot.

On hillslopes, stand age increased with slope and distance from the coast and decreased with elevation (Table 2.3). Hillslope sites on convex slopes tended to be located further from the nearest old-growth patch than sites on convex slopes, although this relationship was relatively weak ($R^2 < 0.1$). In riparian areas the probability of mass movement decreased with increasing stream order. The probability of flooding increased as slope curvature became more negative. Negative curvature indices were characteristic of second through fourth- order streams where the valley floor was tightly constrained by the surrounding hillslopes. Curvature indices approached zero (indicating a relatively flat surface) along first-order streams, where the 30 m DEM did not distinguish the narrow stream channels, and along third and fourth order streams with wide, unconstrained valley floors. Distance from the nearest old growth patch was positively correlated with distance from the coast for the riparian sites. None of the other disturbance variables exhibited a statistically significant relationship with environmental variables.

Mean basal area and stand density were almost twice as high on hillslopes as in riparian areas (Table 2.1). Mean regeneration density was almost five times as high in riparian areas as on hillslopes, but was also much more variable in the riparian areas. Down wood volume, percent shrub cover, and percent hardwood basal area were also highest in riparian areas. Mean basal area of *A. macrophyllum* was higher in riparian areas than on hillslopes, while the mean basal area of *P. menzeisii* was over eight times higher on hillslopes than in riparian areas. *Berberis nervosa* (Oregon grape), *Gaultheria shallon* (salal), and *Rubus ursinus* (trailing blackberry) all had highest cover on hillslopes, while *Menziesia ferruginea*

(fool's huckleberry), *Ribes bracteosum* (stink currant), and *R. spectabilis* had highest cover in riparian areas.

While overall advance regeneration density was highest in riparian areas, this pattern changed with distance from the coast. Within five km of the coast seedling and sapling densities were almost an order of magnitude higher in riparian areas than on hillslopes (Table 2.4). At sites more than five km from the coast, however, riparian areas and hillslopes both had low densities of seedlings and saplings. *P. sitchensis* and *T. heterophylla* comprised the majority of the seedling and sapling banks; contributions of other tree species were relatively minor (Table 2.5). Most advance regeneration within five kilometers of the coast was *P. sitchensis*, although *T. heterophylla* percentages were also high. Most seedlings and sapling further than five km from the coast were *T. heterophylla*. *P. sitchensis* comprised only a small portion of the regeneration bank at inland sites, with the exception of *P. sitchensis* saplings in riparian areas.

Species Composition Patterns

The stepwise RDA of hillslope community composition selected distance from the coast, elevation, distance from remnant patches, slope curvature, and growing season solar radiation as explanatory variables, accounting for 27% of the total variability. The first hillslope axis reflected a gradient from high-elevation inland sites to low elevation sites near the coast (Figure 2.3, Table 2.6). The high-elevation inland sites were dominated by *P. menziesii*, while the low-elevation coastal sites were characterized by *P. sitchensis* and *T. heterophylla* in the tree layer and *Vaccinium ovatum* (evergreen huckleberry) in the understory. We interpreted this axis primarily as a climatic gradient from relatively dry

Table 2.4: Comparison of mean regeneration density per hectare (with standard error in parentheses) on hillslopes and riparian areas by distance from the coast. *P*-values are from two-sample *t*-tests.

	Hillslope	Riparian	*p*-value
Seedlings/ha			
< 5 km from Coast	277.8 (146.9)	2080.9 (561.3)	0.002
> 5 km from Coast	175.1 (82.8)	155.6 (111.8)	0.401
Saplings/ha			
< 5 km from Coast	56.9 (44.7)	264.4 (75.8)	< 0.001
> 5 km from Coast	34.5 (27.7)	24.7 (14.2)	0.344

Table 2.5: Species composition of seedling and saplings computed as a percentage of the total density of seedlings or saplings within each landscape unit. Species composition is computed separately for hillslopes and riparian areas, and for coastal and inland sites.

	< 5 km from Coast		> 5 km from Coast	
	Hillslope	Riparian	Hillslope	Riparian
Seedlings				
Acer macrophyllum	0.0	0.2	0.4	1.4
Alnus rubra	0.0	1.0	0.5	3.8
Picea sitchensis	56.2	70.2	3.1	9.8
Pseudostuga menziesii	4.7	0.7	7.2	0.0
Thuja plicata	0.0	0.4	0.4	0.0
Tsuga heterophylla	39.0	27.6	87.8	84.3
Saplings				
Acer macrophyllum	0.0	1.2	0.0	0.0
Alnus rubra	0.0	7.8	2.1	0.0
Picea sitchensis	75.4	39.7	0.0	34.7
Pseudostuga menziesii	0.0	0.0	0.0	0.0
Thuja plicata	0.0	0.0	0.0	7.6
Tsuga heterophylla	24.6	51.0	95.1	53.7

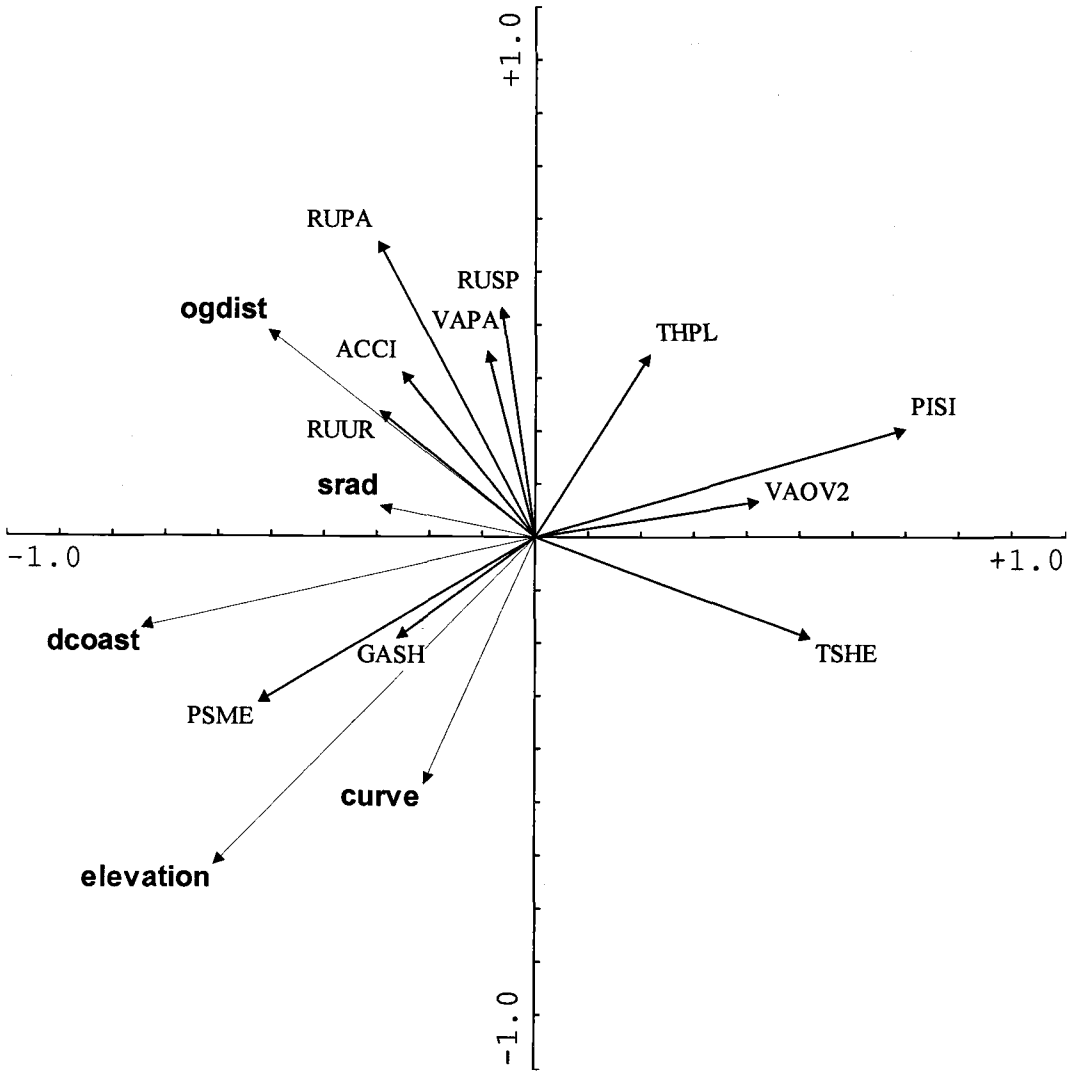


Figure 2.3: Redundancy analysis biplot for hillslope species composition. Bold labels and arrows represent environmental and disturbance variables selected using a forward stepwise method with $p < 0.05$ required to enter the model: **curve**=slope curvature, **dcoast**=distance from the coast, **elevation**=elevation above sea level, **ogdist**=distance from nearest old-growth patch, and **srad**=growing season solar radiation. Capitalized labels represent species with 10 % or more of their total variability explained by the first two ordination axes: ACCI=*Acer circinatum*, GASH=*Gaultheria shallon*, PISI=*Picea sitchensis*, PSME=*Pseudotsuga menziesii*, RUPA=*Rubus parviflorum*, RUSP=*Rubus spectabilis*, RUUR=*Rubus ursinus*, THPL=*Thuja plicata*, TSHE=*Tsuga heterophylla*, VAPA=*Vaccinium parvifolium*, and VAOV2=*Vaccinium ovatum*.

Table 2.6: Correlation of species, environment, and disturbance variables with the first two axes of the hillslope and riparian community composition RDAs. The *p*-value for each axis is derived from a permutation test of the strength of association between the ordination axis and the vegetation variables. Underlined variables represent the three strongest correlations between vegetation variables and the ordination axes. Boldface numbers represent the three strongest correlations between explanatory variables and the ordination axes.

	Hillslope		Riparian	
	Axis 1	Axis 2	Axis 1	Axis 2
% Variance Explained	10.3	7.9	18.0	13.6
p-value	0.001	0.002	0.001	0.002
Species				
Acer macrophyllum	-0.11	0.26	0.05	-0.46
Alnus rubra	-0.01	0.26	0.30	0.05
Picea sitchensis	0.70	0.20	-0.77	0.17
Pseudostuga menziesii	-0.52	-0.31	0.71	0.44
Thuja plicata	0.21	0.34	0.02	-0.01
Tsuga heterophylla	0.52	-0.19	-0.52	0.33
Acer circinatum	-0.25	0.31	-0.03	-0.31
Berberis nervosa	-0.14	-0.06	0.26	0.76
Gaultheria shallon	-0.26	-0.19	0.03	0.65
Menziesia ferrungia	0.16	0.14	-0.49	0.23
Ribes bracteosum	NA	NA	0.41	-0.23
Rubus parviflorous	-0.30	0.55	-0.22	0.14
Rubus spectabilis	-0.06	0.43	0.70	0.13
Rubus ursinus	-0.29	0.24	NA	NA
Sambucus racemosa	0.16	0.10	-0.02	-0.13
Vaccinium ovatum	0.42	0.07	-0.63	0.21
Vaccinium parvifolium	-0.09	0.35	0.08	0.57
Environment				
Elevation	**-0.61**	**-0.62**	**0.88**	0.44
Distance from coast	**-0.74**	-0.17	**0.94**	-0.34
Slope Curvature	-0.21	**-0.46**	-0.24	0.55
Solar Radiation	-0.29	0.06	0.08	0.54
Topographic Moisture	0.42	0.11	0.02	**-0.67**
Slope Angle	-0.04	0.37	0.58	**0.74**
Slope Position	-0.19	**-0.75**	NA	NA
Distance from stream	-0.37	-0.44	NA	NA
Stream Order	NA	NA	-0.28	**-0.81**
Valley Floor Width	NA	NA	**-0.58**	-0.27
Disturbance				
Stand age	-0.03	0.24	-0.29	0.18
Remnant trees	0.03	-0.19	-0.19	0.03
Distance from Old Growth	**-0.50**	0.39	-0.50	0.39
Multiple cohorts	-0.18	-0.12	-0.09	0.05
Mass movement	-0.04	0.32	0.02	0.59
Windthrow	0.33	-0.20	NA	NA
Flooding	NA	NA	0.12	-0.64

inland environments with high annual temperature variability to a moister maritime climate with lower annual temperature variability (Hemstrom and Logan 1986).

The first axis was also correlated with distance from remnant old-growth patches; both *T. heterophylla* and *P. sitchensis* decreased with distance from the nearest old-growth patch (Figure 2.4). Multiple regression analysis revealed that *T. heterophylla* basal area had a statistically significant relationship with distance from old growth even when relationships with other environmental and disturbance variables were taken into account (partial R^2=0.16, $p < 0.001$ with distance from the coast and presence of remnant trees already included in the model). The relationship between *P. sitchensis* and distance from old growth, however, was confounded by correlation with environmental and disturbance variables (partial R^2=0.03, p=0.15 with distance from the coast, distance from streams, and presence of windthrow already included in the model).

P. sitchensis and *T. heterophylla* are both fire-sensitive (Agee 1993), and we observed that remnant trees of these species occurred only within the old-growth patches where historical fires presumably burned at low severity. *P. menziesii* is a comparatively fire-tolerant (Agee 1993), and individual remnant trees of this species were dispersed more widely across the study area. Based on these observations, we hypothesized that most of the *T. heterophylla* and *P. sitchensis* that survived the historical fires to disseminate seeds were concentrated in areas of low fire severity that are reflected in the current distribution of remnant old-growth patches. Because the seed rain of both *T. heterophylla* and *P. sitchensis* into forest openings decreases greatly within 1000 m of the source (Pickford 1929, Issac 1930, Harris 1967) we further hypothesized that the current distributions of these species arose in part because of seed-limited recruitment related to the spatial pattern of old-growth patches.

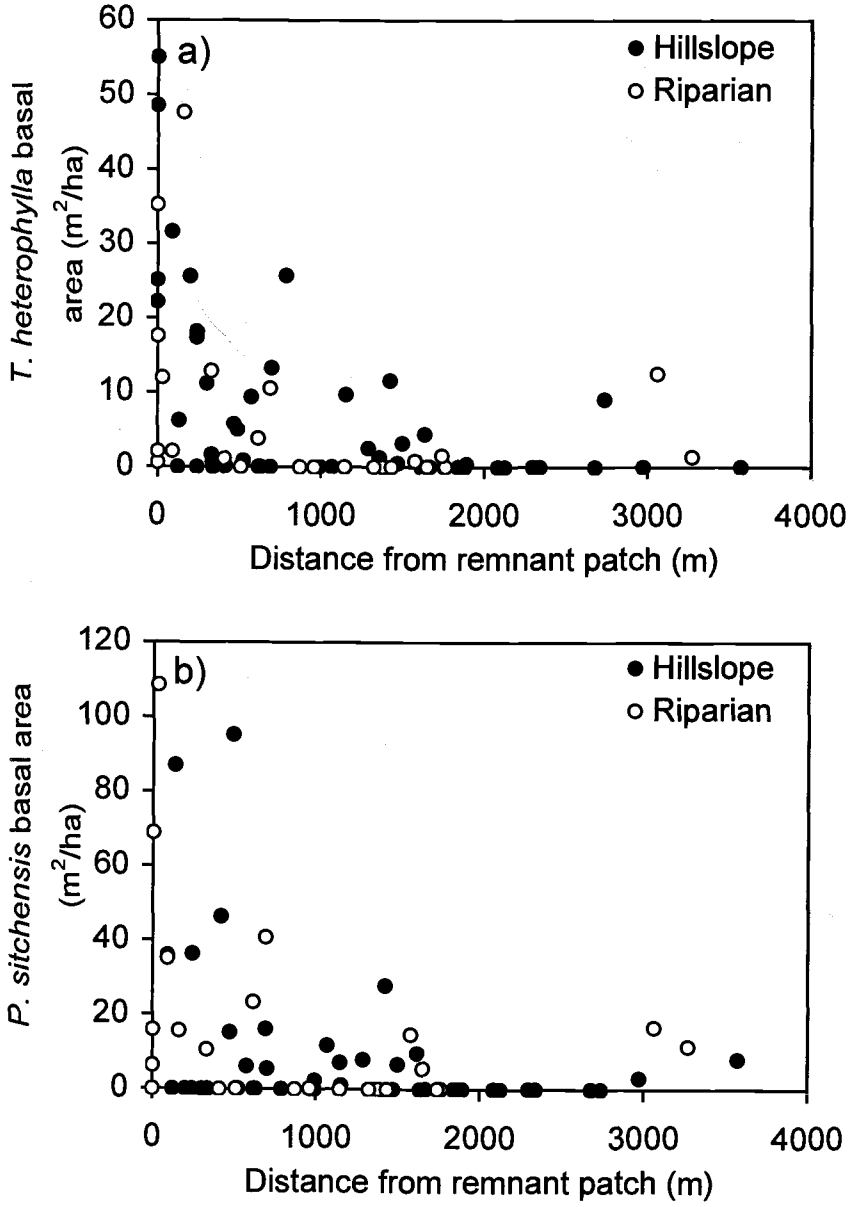


Figure 2.4: Basal area per hectare of a) *T. heterophylla* and b) *P. sitchensis* as a function of distance from the nearest old-growth patch.

The second hillslope axis reflected a gradient from high-elevation ridgetop sites with convex slopes to low-elevation, lower-hillslope sites with concave slopes (Figure 2.3, Table 2.6). We interpreted this axis as a topographic moisture gradient. Moist sites were characterized by *T. plicata* in the tree layer and high cover of shrubs such as *Rubus parviflorum* (thimbleberry), *R. spectabilis*, *Vaccinium parvifolium* (red huckeberry), and *Acer circinatum* (vine maple). In contrast, drier ridgetop sites were dominated by *P. menziesii* in the tree layer and had low cover of all shrub species.

When the riparian sites were considered, stepwise RDA selected distance from the coast, elevation, and channel gradient as explanatory variables. These variables accounted for 37% of the variability in riparian community composition. The first riparian axis was similar to the first hillslope axis, reflecting a gradient from low-elevation coastal sites to high-elevation inland sites (Figure 2.5, Table 2.6). The low-elevation coastal riparian sites tended to have wide valley floors and low stream gradients and were dominated by *P. sitchensis* and *T. heterophylla* in the tree layer and *M. ferruginea* and *V. ovatum* in the shrub layer. The high-elevation inland sites had narrower valley floors and steep gradients and were characterized by high levels of *A. rubra* and *P. menzeisii* in the tree layer and *R. bracteosum* and *R. spectabilis* in the shrub layer. We interpreted this axis as a maritime to inland climatic gradient similar to that described for the hillslope ordination. Climate was to some degree confounded by stream size, however, since the largest, highest-order streams were found near the coast. This gradient was also correlated with distance from old-growth patches (Table 5), suggesting the seed dispersal limitations played a role in structuring the distribution of fire-sensitive tree species in riparian forests.

The change from *P. sitchensis* to *P. menziesii* dominated forests with distance from the coast occurred more rapidly on hillslopes than in riparian areas (Figure 2.6). In riparian

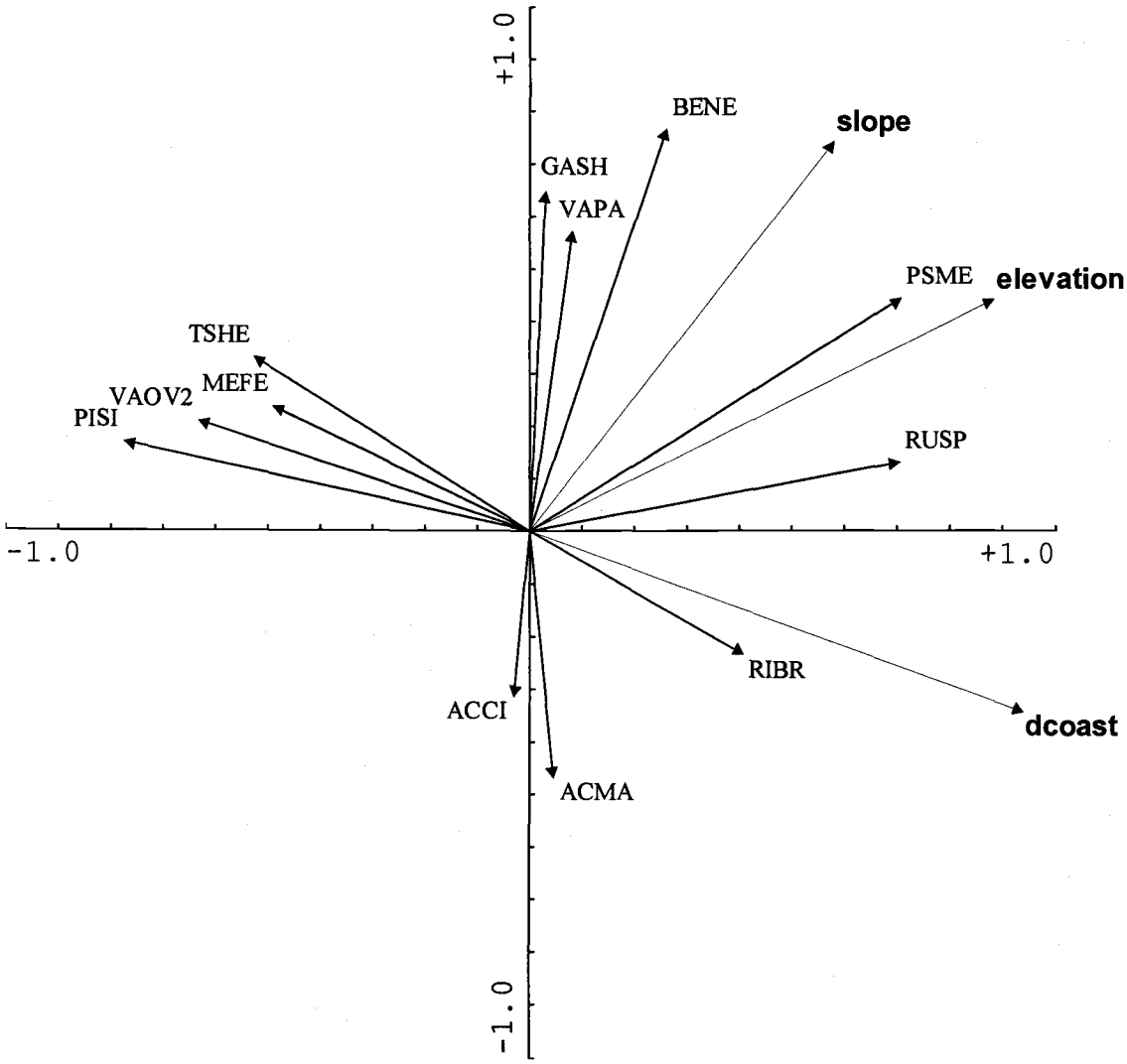


Figure 2.5: Redundancy analysis biplot for riparian species composition. Bold labels and arrows represent environmental and disturbance variables selected using a forward stepwise method with $p < 0.05$ required to enter the model: **dcoast**=distance from the coast, **elevation**=elevation above sea level, and **slope**=channel gradient. Capitalized labels represent species with 10 % or more of their total variability explained by the first two ordination axes: ACCI=*Acer circinatum*, ACMA=*Acer macrophyllum*, *BENE=Berberis nervosa*, GASH=*Gaultheria shallon*, MEFE=*Menziesia ferrungia*, PISI=*Picea sitchensis*, PSME=*Pseudotsuga menziesii*, RIBR=*Ribes bracteosum*, RUSP=*Rubus spectabilis*, THPL=*Thuja plicata*, TSHE=*Tsuga heterophylla*, and VAOV2=*Vaccinium ovatum*.

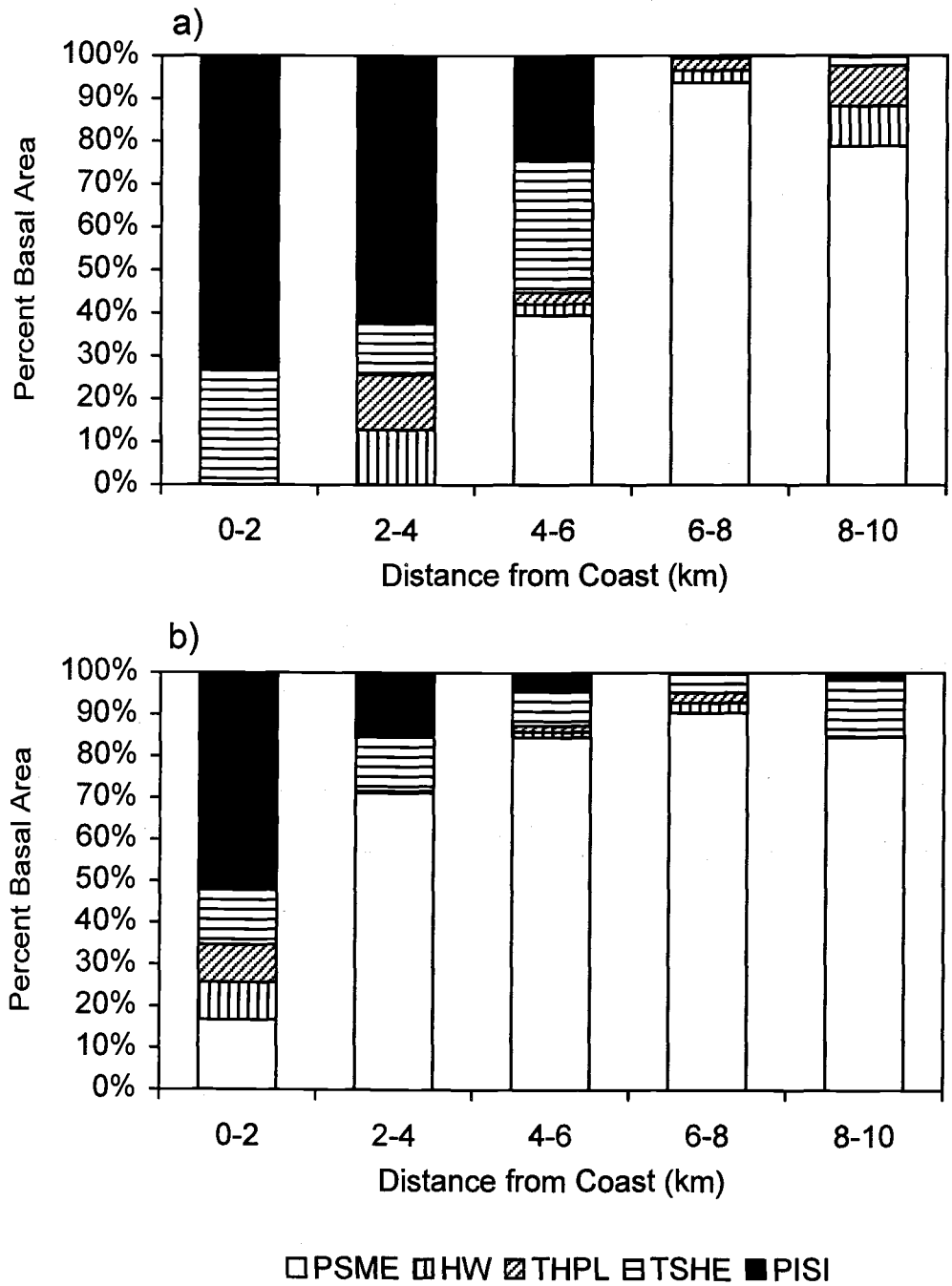


Figure 2.6: Overstory species composition computed as a percentage of the total basal area within each landscape unit as a function of distance from the coast for a) riparian areas and b) hillslopes.

areas, *P. sitchensis* was the dominant conifer species from the coast up to four km inland. *P. menzeisii*, in contrast, was not found in riparian areas less than four km from the coast, but dominated riparian forests more than six km inland. On hillslopes, however, the proportion of *P. sitchensis* basal area decreased more rapidly with distance from the coast. *P. menziesii* was present on hillslopes at all distances from the coast, and became the dominant species at sites just two km inland.

The second riparian axis reflected a gradient from low-gradient streams to high-gradient streams (Figure 2.5, Table 2.6). The low-gradient streams were mostly high-order streams with high occurrences of flood disturbance, and were dominated by *A. macrophyllum* in the tree layer and *A. circinatum* in the shrub layer. High-gradient, low-order streams had high occurrences of mass movement disturbance. Plant communities along these streams were dominated by species usually associated with hillslope environments, including *P. menziesii*, *G. shallon*, and *B. nervosa*. The prevalence of these species may have reflected the fact that sample sites along the lower-order streams tended to encompass more of the surrounding hillslopes than the valley floor itself.

Forest Structure Patterns

The stepwise RDA of the hillslope forest structure selected stand age, presence of remnants, distance from remnants, slope curvature, and presence of windthrow as explanatory variables, accounting for 30% of the structural variability. The first hillslope axis reflected a gradient from young stands and sites far from old-growth patches to older stands, stands with old-growth trees, and sites close to old-growth patches (Figure 2.7, Table 2.7). Basal area, large tree density and standard deviation of dbh had the strongest relationships with this axis; all increased with stand age and proximity to old-growth patches. Percent shade-tolerant basal

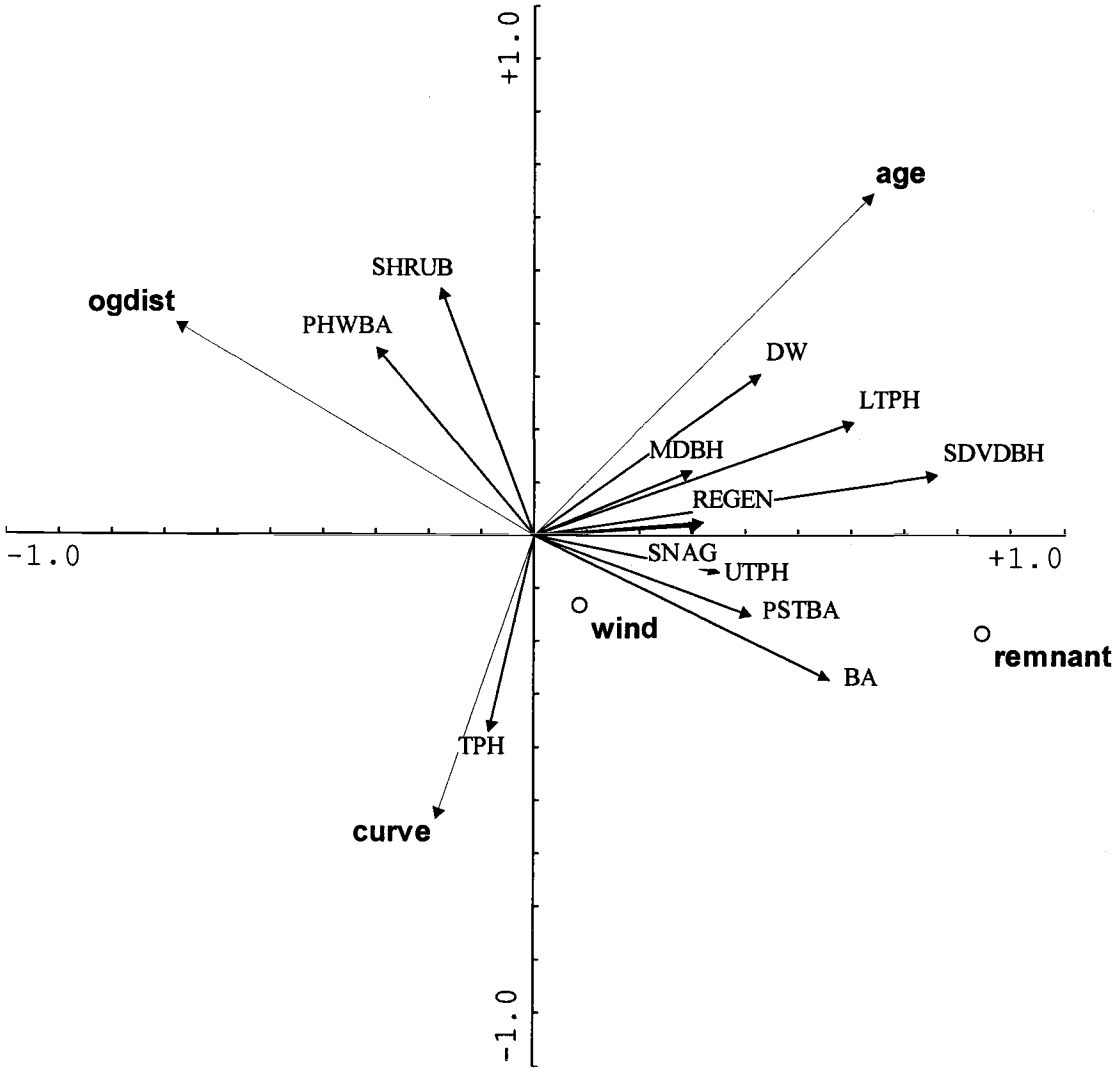


Figure 2.7: Redundancy analysis biplot for hillslope forest structure. Bold labels and arrows represent environmental and disturbance variables selected using a forward stepwise method with $p < 0.05$ required to enter the model: **age**=stand age, **curve**=slope curvature, **ogdist**=distance from nearest old-growth patch, **remnant**=indicator variable for sites with remnant old-growth trees, and **wind**=indicator variable for sites with windthrow. Capitalized labels represent structure variables with 10 % or more of their total variability explained by the first two ordination axes: BA=basal area, DW=down wood volume, LTPH=large tree per hectare, MDBH=mean diameter at breast height, PHWBA=percent hardwood basal area, PSTBA=percent shade-tolerant basal area, SDVDBH=standard deviation of diameter at breast height, SHRUB=shrub cover, SNAG=large (>50 m dbh) snag density, TPH=total trees per hectare, and UTPH=understory trees per hectare.

Table 2.7: Correlation of structure, environment, and disturbance variables with the first two axes of the hillslope and riparian forest structure RDAs. The *p*-value for each axis is derived from a permutation test of the strength of association between the ordination axis and the vegetation variables. Underlined variables represent the three strongest correlations between vegetation variables and the ordination axes. Boldface numbers represent the three strongest correlations between explanatory variables and the ordination axes.

	Hillslope		Riparian	
	Axis 1	Axis 2	Axis 1	Axis 2
% Variance Explained	17.7	6.2	19.3	8.2
p-value	0.001	0.032	0.003	0.025
Structural Variable				
Tree Density	-0.84	-0.37	-0.32	0.29
Mean dbh	0.30	0.12	-0.12	-0.11
Std. Dev. of dbh	0.76	0.11	-0.56	-0.38
Basal Area	0.53	-0.27	-0.55	0.02
Large (> 100 cm dbh) Tree Density	0.62	0.21	-0.49	-0.04
Understory Tree Density	0.35	-0.07	-0.33	0.30
Regeneration Density	0.31	0.02	-0.66	-0.06
Percent High Shrub Cover	-0.18	0.46	0.65	0.44
Large (> 50 cm dbh) Snag Density	0.32	0.03	-0.21	0.15
Down Wood Volume	0.43	0.30	-0.07	0.31
Percent Shade Tolerant Basal Area	0.41	-0.15	-0.35	0.40
Percent Hardwood Basal Area	-0.30	0.35	0.43	-0.42
Environment				
Elevation	-0.26	-0.13	**0.79**	0.35
Distance From Coast	0.11	0.18	**0.98**	-0.21
Slope Curvature	-0.18	**-0.53**	-0.46	0.43
Solar Radiation	0.33	-0.16	-0.20	0.21
Topographic Moisture	0.08	0.18	0.20	**-0.73**
Slope Angle	0.11	0.39	0.30	**0.74**
Slope Position	-0.11	**-0.52**	NA	NA
Distance from stream	0.03	-0.43	NA	NA
Stream Order	NA	NA	-0.23	**-0.97**
Valley Floor Width	NA	NA	-0.66	-0.46
Disturbance				
Stand age	**0.64**	**0.64**	-0.46	0.18
Remnant Patch	**0.81**	-0.18	-0.53	0.20
Distance from Old Growth	**-0.68**	0.40	**0.67**	-0.52
Multiple cohorts	-0.11	0.22	-0.12	-0.18
Mass movement	0.34	0.39	-0.10	0.69
Windthrow	0.15	-0.22	NA	NA
Flooding	NA	NA	0.19	-0.29

area, mean dbh, large snag density, and regeneration density also increased with stand age and proximity to old-growth patches, but had weaker correlations with the ordination axis. Large dominant trees, a wide range of tree sizes, high densities of large snags, and down wood volumes are all characteristics of old-growth forests in the Pacific Northwest (Spies and Franklin 1991). We therefore interpreted this axis as a gradient of increasing late-successional structure development with forest age. The relationship with distance from old-growth patches reflected the spatial association between *T. heterophylla* and fire refugia discussed in the previous section. Sites close to old-growth patches with abundant *T. heterophylla* tended to have a high percentage of shade-tolerant basal area. These sites also had high densities of suppressed, understory *T. heterophylla* that increased the range of tree sizes.

The second hillslope axis represented a complex gradient of age structure and topography. Younger stands and sites on convex landforms were generally found on upper slope positions and had high-density conifer-dominated overstories with high basal area and few shrubs. Older stands and sites on concave landforms were found at lower slope positions and had low overstory densities with a high proportion of hardwoods, low basal area, and a dense shrub layer. We interpreted this axis as a topographic moisture gradient, with hardwoods and shrubs favored on concave landforms that collect soil moisture, and conifer stands with few shrubs favored on convex landforms that disperse soil moisture. Mixed hardwood/conifer stands had lower density and basal area than conifer stands because many of the older hardwood patches have begun to senesce over the past few decades. The correlation with stand age probably the fact that the dry convex ridges experienced more reburns than the more concave lower hillslopes, and therefore were younger in age. The fourth ordination axis (not shown) reflected a gradient from sites with windthrow and high volumes of down wood to sites without windthrow and low levels of down wood.

In the riparian areas, stepwise RDA selected distance from the coast and stream order as explanatory variables. These variables accounted for 28% of the variation in riparian forest structure. The first riparian axis reflected a gradient from coastal to inland sites (Figure 2.8, Table 2.8). The coastal sites tended to occur at low elevations along streams with wide valley floors, and were generally closer to old-growth patches than the inland sites. Structural variation along this gradient was similar to that along the first hillslope gradient; basal area, overstory density, large tree density, understory tree density, standard deviation of dbh, regeneration density, and percent shade-tolerant basal area were all highest near the coast and decreased with distance from the coast. Percent shrub cover and percent hardwood cover, in comparison, were lowest near the coast and increased with distance inland. We interpreted this axis as a gradient of late-successional structure development similar to that described for the hillslope sites. Compared to the hillslope ordination, the riparian old growth gradient had weaker correlations with disturbance variables and a very strong relationship with the coast-to-inland climatic gradient.

The second riparian axis reflected a gradient from high to low-order streams (Figure 5, Table 6). High-order streams had wider valley floors, higher topographic moisture indices, and lower incidence of mass movement than low-order streams. Standard deviation of dbh and percent hardwood basal area were lowest in low-order streams and increased with stream order. In contrast, percent shrub cover, understory trees per hectare, down wood volume, and percent shade-tolerant basal area were highest in the low-order streams. This gradient reflected a variety of ecological factors that changed with stream size and gradient. High proportions of hardwoods along high-order streams probably reflected the abundance of *A. rubra* patches that established after floods, along with large *A. macrophyllum* that were mostly restricted to broad valley floors. The mixtures of smaller *A. rubra* with larger

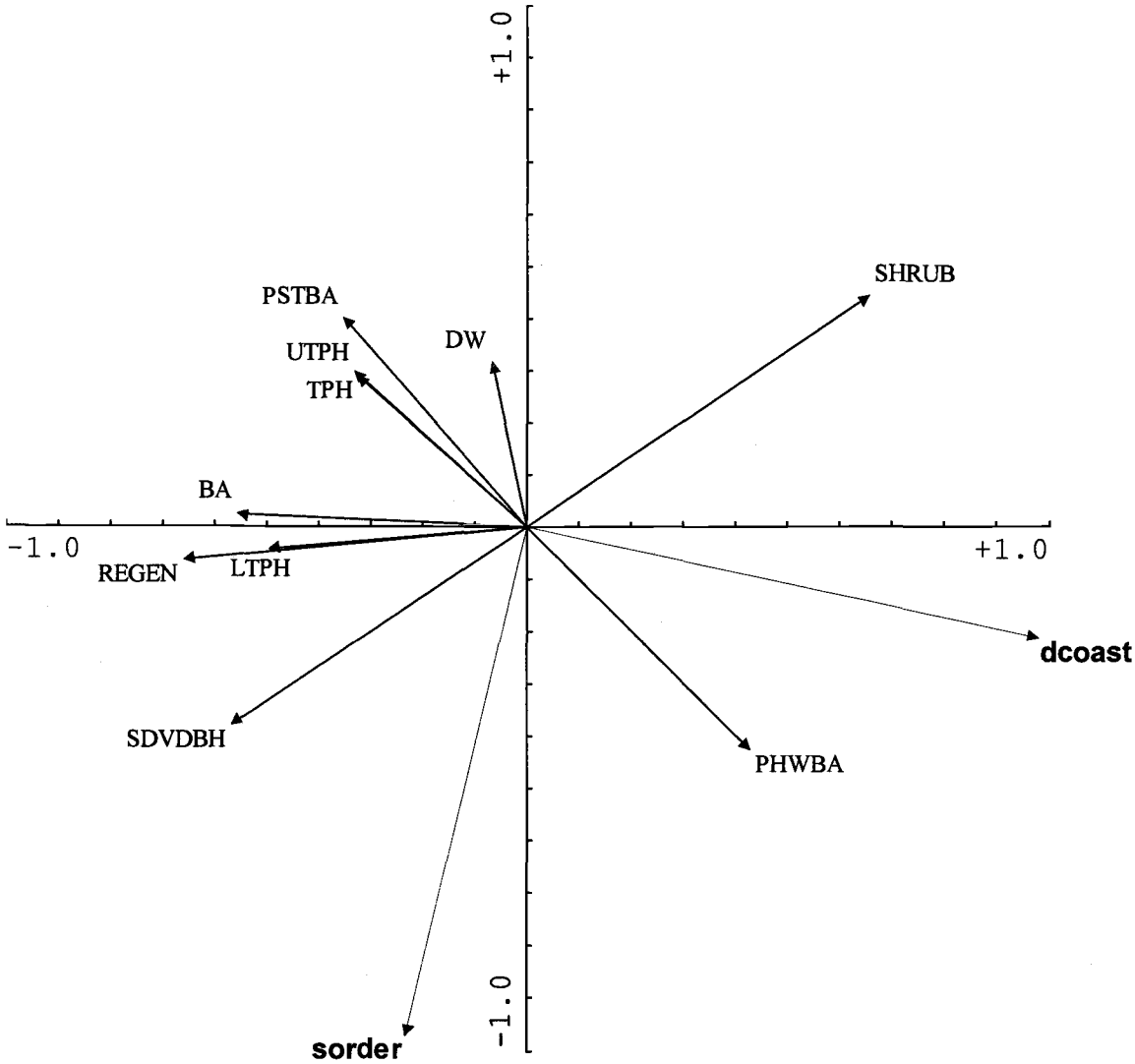


Figure 2.8: Redundancy analysis biplot for riparian forest structure. Bold labels and arrows represent environmental and disturbance variables selected using a forward stepwise method with $p < 0.05$ required to enter the model: **dcoast**=distance from the coast and **sorder**=stream order. Capitalized labels represent structure variables with 10 % or more of their total variability explained by the first two ordination axes: BA=basal area, DW=down wood volume, LTPH=large tree per hectare, PHWBA=percent hardwood basal area, PSTBA=percent shade-tolerant basal area, and REGEN=tree regeneration density, SDVDBH=standard deviation of diameter at breast height, SHRUB=shrub cover, TPH=total trees per hectare, UTPH=understory trees per hectare.

A. macrophyllum and conifers may have accounted for the greater variability in tree sizes along the high-order streams. Higher amounts of shade-tolerant conifers and understory trees (mostly shade-tolerant conifers) along low-order streams may simply have reflected the higher overall proportion of conifers in these environments. Browsing by elk and deer may have reduced the density of shrubs along high-order streams, while mass movement disturbances probably increased down wood input from hillslopes into low-order streams.

Relative Importance of Disturbance and Environment

On hillslopes, environmental variables alone accounted for 74 percent of the explained variation in species composition, while disturbance variables alone accounted for 26 percent (Figure 2.9). Environmentally structured disturbance variables did not account for any of the explained variation in hillslope species composition. In contrast, disturbance variables alone accounted for 85 percent of the explained variation in hillslope forest structure. Environment alone accounted for 12 percent of the explained variation in hillslope forest structure, and environmentally structured disturbance variables accounted for the additional 3 percent. In the riparian areas, environmental variables alone accounted for 68 percent of the explained variability in species composition, while disturbance variables alone accounted for 21 percent and environmentally structured disturbance variables accounted for 11 percent. When riparian forest structure was considered, environmental variables alone accounted for 48 percent, disturbance variables alone accounted for 29 percent, and environmentally structured disturbance variables accounted for 22 percent of the explained variability.

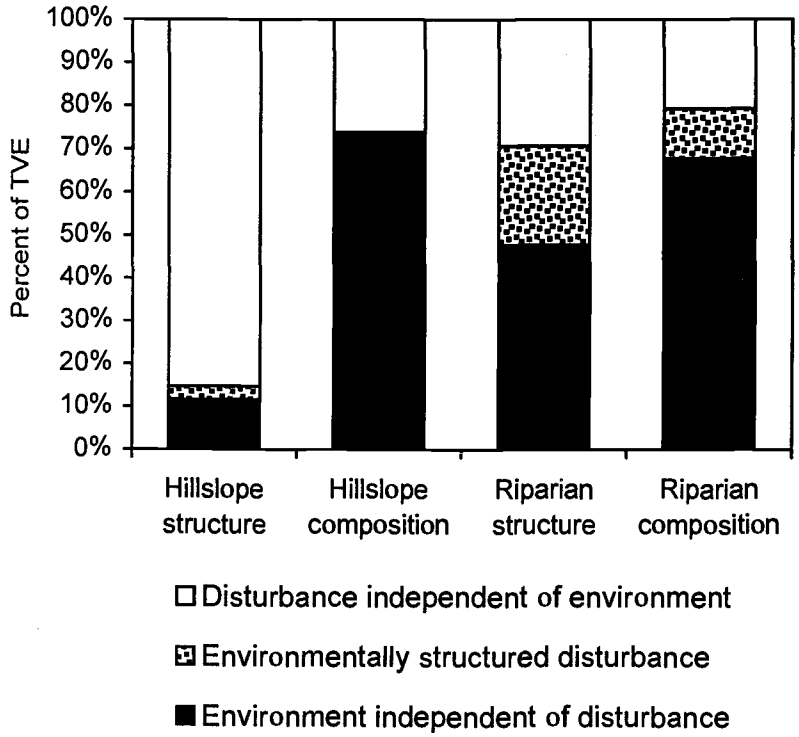


Figure 2.9: Percentage of the total variation explained (TVE) accounted for by disturbance and environment variables in the redundancy analysis ordinations. Variation partitioning was carried out using the method of Okland and Eilertsen (1994) for hillslope forest structure, hillslope species composition, riparian forest structure, and riparian species composition.

Discussion

Recent Fire History

Fire history in the Cummins Creek Wilderness was more complex than we had originally expected. Contrary to our initial hypothesis, old-growth remnants were no more common in riparian areas or moist sites than in other parts of the landscape. The distribution of overstory tree ages along with historical evidence suggested that many parts of the landscape reburned several times after a large catastrophic fire in the mid-19th century. The rarity of multiple cohort stands indicated that these reburns were mostly stand replacing fires that killed all of the young trees on a site, while the variation in forest age distribution with topographic position suggested that riparian areas experienced fewer reburns than hillslopes. Stand age on hillslopes increased with slope and decreased with elevation, indicating the most recently burned stands were found on the gently sloped, high-elevation ridges. These patterns reflect a broader trend of higher fire frequency and severity on upper than lower hillslopes in the Central Coast Range (Impara 1997).

The occurrence of multiple reburns affects our interpretation of relationships between stand age and vegetation characteristics. Most importantly, the range of stand ages cannot be interpreted as a true chronosequence. The oldest sites, with breast height ages greater than 120 years, probably established shortly after the 1849 fire following a preceding fire-free period of 200 years or more. Younger sites with breast height ages ranging from 70 to 120 experienced one or more additional burns after 1849. These multiple burns within a relatively short time probably affected soil characteristics, availability of seed sources, and density and composition of competing vegetation in addition to simply delaying stand establishment (Agee 1993).

We found that percent shade-tolerant basal area, understory tree density (predominantly shade-tolerants), and advance regeneration density all increased with age in hillslope forests, as expressed by the first RDA axis in the hillslope structure ordination. Schrader (1998) similarly found that *T. heterophylla* overstory and regeneration density increased with stand age, and concluded that gradual accumulation of seedlings and saplings over time since disturbance was a critical factor influencing the size of the advance regeneration bank. Our fire history results suggest an alternative explanation. If younger stands were subjected to multiple burns prior to establishment, then these burns may have reduced the densities of shade-tolerant, fire intolerant species such as *T. heterophylla*. Low seed availability from mature shade-tolerants could then be another explanation for low regeneration density in the younger stands. Several other studies have concluded that multiple reburns after a stand-replacing fire lead to decreased amounts of shade-tolerant trees in the post-fire forest (Klopsch 1985, Poage 1995, Gray and Franklin 1997). It is not possible to disentangle the influences of time since disturbance and frequency of reburns in the present case, and we suspect that both of these factors are reflected in the stand age variable.

Several researchers have documented increases in fire frequency during the mid to late 19th century, concurrent with European settlement (Weisberg 1998). These increases have been attributed to increased ignitions from land-clearing fires set by settlers, but may also have been caused by the warmer, drier climate that prevailed at the end of the Little Ice Age (Weisberg 1998). Although we found no direct historical references to human-caused fires in our study area, several lines of evidence suggest that burning by settlers may have contributed to the multiple fires in the Cummins Creek Wilderness. Our model of stand age on hillslopes predicted younger stands near the coast, contradicting the general assumption that moist, coastal forests rarely burn (Agee 1993). The younger stands near the coast may instead

reflect higher ignition rates from fires set for land clearing. Several homesteads were established along the coast, just to the west of our study area, and settlers in this area are known to have used fire to clear land and maintain pasture for sheep and cattle (Hays 1976, Bogue and Yunker 1991). If burning occurred during the summer months, it is possible that the prevailing westerly winds could have carried the fires inland and burned portions of our study area.

Riparian Forests

Differences between riparian and hillslope forests were mostly similar to those reported previously (McGarigal and McComb 1992, Hayes et al. 1996, Pabst and Spies 1998, Pabst and Spies in press), supporting the general assumption that riparian areas in the Coast Range have sparser overstories and denser shrub layers than hillslopes. Although riparian forests had low densities of large conifers and low overstory basal areas, they had higher volumes of down wood than the hillslopes. Flooding and mass movement disturbances in the riparian areas may have led to higher mortality of overstory conifers compared to the more stable hillslopes. Because these disturbances typically kill trees by undercutting or uprooting (Gregory et al. 1991), the dead boles enter the coarse woody debris pool as down logs rather than snags.

Down wood accumulation in the riparian areas may also reflect the stream system's role in collecting and transporting woody debris. Much of the wood and sediment in Coast Range streams enters the riparian network through landslides that occur in "bedrock hollows" near channel headwaters (Benda 1990). This material moves through the steep, low-order stream channels during episodic debris flows, often requiring several such disturbance events to reach larger, low-gradient streams. A particular stream reach can thus accumulate wood

from upstream forests as well as from the forests immediately adjacent to it. Our field observations supported this hypothesis. Much of the down wood in the low-order riparian areas was concentrated in the stream channel itself, and was oriented parallel to the direction of flow. We interpreted these patterns as evidence that the wood had been transported from upstream. Recently fallen trees, in comparison, tended to span the channel with a perpendicular or oblique orientation. We also observed debris fans of wood and sediment located downstream of many tributary junctions along the mainstems of Cummins and Bob Creeks. A recent survey found that 48% of the wood along the main channel of Cummins Creek had been transported from upstream (G. Reeves, personal communication).

Previous research has emphasized the scarcity of regeneration in Coast Range riparian areas (Minore and Weatherly 1994, Hibbs and Giordano 1996, Pabst and Spies in press), and we initially expected that riparian areas would have less advance regeneration than hillslopes because of intense shrub competition and lack of seed sources. Although the amount of regeneration we found in these riparian forests was indeed low at our inland sites (> 5 km from the coast), the amount of regeneration on hillslopes was not significantly higher. Basal area of *T. heterophylla*, the predominant species of tree regeneration at inland sites, was similar in riparian areas and on hillslopes suggesting that seed availability may have been a limiting factor in both portions of the landscape. Relatively dense canopies and low amounts of down wood may also have limited regeneration opportunities in the hillslope forests.

Advance regeneration density along coastal streams was actually higher than on coastal hillslopes, and was an order of magnitude higher than along inland streams. One possible reason for these high regeneration levels is the unique environment of the coastal riparian areas. Summer fog along the coast reduces evaporative demand and contributes precipitation in the form of fog drip (Franklin and Dyrness 1988). These conditions are highly

conducive to the regeneration and survival of drought-sensitive species such as *P. sitchensis* and *T. heterophylla* (Minore 1979). Fog often extends furthest inland along coastal river valleys (Franklin and Dyrness 1988) and may partly explain why regeneration densities were so much higher in the coastal riparian areas than on the adjacent hillslopes. Numerous *P. sitchensis* and *T. heterophylla* seed sources along with low shrub cover compared to inland riparian areas probably also contributed to the abundant regeneration along coastal streams.

Landscape Patterns

No single ecological mechanism accounted for all components of watershed-scale forest patterns within the Cummins Creek Wilderness. Environmental constraints, disturbance history, and dispersal limitations all had a role in shaping the current landscape. As in other studies of forest vegetation in the Pacific Northwest (Fonda and Bliss 1969, Zobel et al. 1976, DelMoral and Watson 1978, Ohmann and Spies 1998) we found that climate was an important factor influencing community composition. Although we did not directly incorporate measurements of temperature, precipitation, or other climatic variables into our ordination, we interpreted the coast to inland gradients as reflecting change from a cool maritime climate with low annual temperature variability and low growing season moisture stress to warmer inland environments with higher annual temperature variability and high levels of summer moisture stress. If dominance of *P. sitchensis* in the overstory layer is accepted as an indicator of maritime climates (Franklin and Dyrness 1988), we can infer that the coastal influence extends between four and six km inland along the stream valley, but no further than two km inland on the hillslopes.

Although topography was previously found to have only a weak relationship with regional vegetation patterns in Oregon (Ohmann and Spies 1998) we found strong correlations

between topography and vegetation in our study area. On hillslopes, both forest community composition and forest structure varied along a topographic gradient related to slope position and curvature. In riparian areas, forest structure and composition both varied along gradients related to stream order, stream gradient, and valley floor width. We suspect that the relatively small extent of our study area may have enhanced our ability to detect relationships between topography and vegetation. When these relationships are examined over broader areas, the particular species or structures associated with a given topographic position may vary depending on the macroclimatic setting. Thus, while topographic variables explain little regional variability in community composition, they still may play an important role in structuring forest patterns within a given watershed.

Decreases in the basal area of two fire sensitive tree species (*T. heterophylla* and *P. sitchensis*) with distance from old-growth patches suggested that recruitment limitations arising from the patchy distribution of remnant seed sources have also played a role in structuring forest community patterns at the watershed scale. Several studies have documented decreased seedling establishment with distance from seed sources (Harris 1967, Johnson 1988, Myster and Pickett 1992) and our results provide additional evidence that such recruitment limitations may have a persistent influence on forest patterns. These results must be interpreted cautiously because they are derived from correlations obtained within a single study area. We can hypothesize, however, that similar situations where multiple reburns have created isolated patches of remnant seed sources might partly account for the patchy distribution of *T. heterophylla* in other portions of the central Coast Range (Schrader 1998).

Disturbance variables derived from stand age structure had the strongest correlations with late-successional structure development in hillslope forests, while the influences of environmental variability were comparatively weak. Our results were similar to successional

trends described in previous studies (Spies and Franklin 1991, Acker et al. 1998). Large tree density, down wood volume, snag density, and variability in tree sizes all increased with age, indicating that forests were becoming more similar in structure to old growth over time. Sites with one or more remnant old-growth trees also had higher values of these variables than sites without remnants, indicating that old-growth structure may develop more rapidly in forests recovering from partial as opposed to catastrophic disturbance. As discussed previously, relationships with stand age must be interpreted cautiously since stand age reflects variation in the number of reburns before stand initiation as well as the time since stand initiation.

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

Because of relatively frequent, patchy disturbances such as floods and debris flows in the riparian zone, we had initially hypothesized that disturbance variables would account for more of the explained compositional and structural variability in riparian areas than on

hillslopes. Instead, we found that the proportion of TVE explained by disturbance variables in riparian areas was equal to or lower than the amount explained on hillslopes. However, this result should not be construed as evidence that disturbance is unimportant in riparian forests. We suspect that it instead reflects the limitations of trying to characterize the complex array of riparian disturbances using only stand age along with indicator variables for other disturbance types. In addition, riparian disturbances may have exerted a strong influence on only a limited subset of our species and structure variables.

Our riparian ordination axes did have strong correlations with physiographic variables describing various aspects of the channel network such as stream order, stream gradient, and valley floor width. The proportion of TVE explained by environmentally structured disturbance variables in riparian areas to some degree reflects the linkages between the physical environment and fluvial disturbances. We hypothesize that physical variables may also reflect some of the heterogeneity of responses to riparian disturbances that were not captured by our indicator variables. For example, an individual flood event might remove the majority of streamside vegetation in a narrow, constrained reach, but disturb less vegetation in a broader, unconstrained reach (Hupp 1982, Grant and Swanson 1995). The degree to which floods influence vegetation also decreases with the height of valley floor landforms above the active channel (Sigafoos 1991, Yanosky 1982). A particular debris flow may only impact vegetation within the narrow stream channel as it moves through steep, low-order riparian areas, but can disturb vegetation over much larger areas as it fans out into wider, low-gradient channels (Swanson et al. 1998). More detailed characterizations of riparian disturbance history will be required to accurately assess the relationships among geomorphology, riparian disturbance and forest vegetation.

Implications for Management and Conservation

Our study constitutes a snapshot of a 4,000 ha landscape at a single point in time. In comparison, the Oregon Coast Range is over 2,000,000 ha in size, and its forests have changed as a result of disturbance and climatic variation over thousands of years (Worona and Whitlock 1995, Wimberly et al. in press). Although our description of vegetation patterns in the Cummins Creek Wilderness provides one potential reference landscape, it is erroneous to infer that all other areas in the Coast Range should have precisely similar patterns. Also, because historical records suggest that burning by settlers played a role in igniting the most recent fires it is possible that the conditions leading up to the establishment of the current forests were unlike those that operated during presettlement times. With these limitations in mind, our study still provides several valuable lessons applicable to forest management and conservation.

Most of the forests in the Cummins Creek Wilderness were established following large, high-severity fires in the late 19th century. Viewed from a regional scale, this landscape might be perceived as a relatively homogeneous block of late-successional forest. Our investigation, however, revealed considerable heterogeneity of both forest structure and composition at the watershed scale. This heterogeneity arose from environmental variability related to topography and distance from the coast, as well as the spatial and temporal patterns of fires, floods, and other historical disturbances. Intensive forest management practices often involve planting a preferred conifer species (usually *P. menziesii*) and controlling hardwoods and shrubs through chemical or mechanical treatments. These activities may serve to homogenize these landscapes relative to the structural and compositional diversity observed in the Cummins Creek Wilderness. Our results provide some indication of the range of habitat variability that might be expected in late-successional coastal watersheds.

Landscape management or restoration strategies that are narrowly based on a simplistic ecological framework may fail to provide the full range of variability found in unmanaged forest watersheds. The predominant approach for watershed-scale management of biodiversity in the Pacific Northwest is currently the use of streamside buffers. Maximum no-harvest buffer widths in the Coast Range vary from 20 feet on private and state lands to 300 feet or more on federal lands (Gregory 1997). This strategy assumes that preserving riparian areas and lower hillslopes in an unmanaged state will maintain biodiversity for the watershed as a whole. Although our research does not disprove this assumption, it indicates that the dry upper hillslopes and ridges may support distinctive forest structures and combinations of plant species. While streamside buffers may help to mitigate some of the impacts of logging on streams, they will probably not provide for the full range of habitat characteristics within a late-successional watershed.

P. Sitchensis-dominated coastal riparian areas had several unique attributes compared to inland riparian forests. The coastal riparian forests supported higher regeneration densities and had a greater degree of late-successional structure than inland riparian forests. The abundant understory regeneration of *P. sitchensis* and *T. heterophylla* near the coast suggest that other coastal riparian sites might have a high potential for rapid development of conifer-dominated, late-successional streamside forests. Inland forests, both in riparian areas and on hillslopes, had comparatively low levels of shade-tolerant regeneration. We hypothesize that in many cases, the current lack of shade-tolerant species has arisen because multiple reburns and dispersal limitations linked to the patchy distribution of remnant seed sources have eliminated much of the *T. heterophylla* in the overstory. Since shade-tolerant species like *T. heterophylla* disperse over short distances under a closed canopy (Schrader 1998), sites without a seed source will develop a multilayered late-successional structure slowly, if at all.

In areas where rapid development of late-successional structure is a goal and shade-tolerant overstory trees are not present, silvicultural manipulations such as thinning and underplanting may be required to achieve the desired result.

CHAPTER 3

Predicting Landscape Patterns of Understory Conifers Using Field Plots, Remote Sensing, and Digital Elevation Models

Michael C. Wimberly and Thomas A. Spies

Abstract

Many unmanaged forests in the Oregon Coast Range established 80-120 years ago following fires, and will begin to develop old-growth structure over the next century. Future rates and pathways of forest development will vary depending on the density of shade-tolerant conifers in the understory. We developed statistical models to predict landscape patterns of understory *Tsuga heterophylla* (western hemlock) and *Picea sitchensis* (Sitka spruce) in the Cummins Creek Wilderness, located on the Oregon coast. These models predicted understory variables measured in field plots as a function of spatially explicit variables derived from Landsat TM imagery, aerial photographs, digital elevation models, and stream maps. Because the models explained only low to moderate amounts of variability, we interpreted the results as qualitative trends rather than precise maps. *P. sitchensis* advance regeneration was most abundant in riparian areas close to the coast. Few hardwood-dominated patches had *T. heterophylla* in the understory, suggesting that many large hardwood patches will succeed to shrub fields rather than stands of shade-tolerant conifers. Areas in and around old-growth remnant patches were more likely to have *T. heterophylla* in the understory than areas located further away from these patches, and will probably develop multilayered canopy structure more rapidly than areas located further from remnant patches. We hypothesized that these remnant patches served as refugia for the fire-sensitive hemlock during historical wildfires during the late 19th and early 20th centuries. Overstory *T. heterophylla* basal area is currently highest in and around the old-growth patches, and these areas serve as foci for *T. heterophylla* dispersal into the landscape. This result suggests that spatial patterns of disturbance and dispersal limitations must be considered in addition to local environmental conditions when predicting the distribution of fire-sensitive species such as *T. heterophylla*.

Introduction

The Oregon Coast Range is a landscape of relatively young forests. Wildfires and timber harvesting have eliminated most of the old-growth forests that existed before European settlement (Bolsinger and Waddell 1993, Congalton et al. 1993). The current low levels of old growth in the Coast Range have led to concern for the viability of native species dependent on late successional habitats (FEMAT 1993). Scientists and land managers are now trying to determine whether new landscape management strategies can protect ecosystem processes and native species while still providing timber and other commodities. Potential approaches to landscape management include protecting reserves within a managed forest matrix (FEMAT 1993), using active management to produce a range of forest structures across the landscape (Oliver 1992), and developing harvest plans based on historical disturbance regimes (Cissel et al. 1998). In order to assess these untested management strategies we need to be able to model forest succession and predict future landscape patterns under a variety of management scenarios.

Our ability to predict landscape change in the Coast Range is currently limited by our lack of knowledge about understory tree regeneration. The abundance of advance regeneration can be an important factor influencing the development of late-successional characteristics in Pacific Northwest conifer forests. As forests mature, overstory canopy gaps are created when wind, disease, insects, or other disturbances kill individual trees or small patches of trees (Spies et al. 1990, Taylor 1990). Because canopy gap formation typically causes only limited disturbance to the forest floor (Spies and Franklin 1989) these gaps are often filled by advance regeneration that was present prior to the disturbance. Conifer forests with abundant shade-tolerant regeneration will thus gradually develop the multilayered canopy structure characteristic of old growth. In stands where understory regeneration is

sparse or absent, canopy gap formation will increase the height and density of the shrub layer (Holah et al. 1993). In these cases, competition from shrubs may limit seedling establishment and multilayered structure will develop slowly if at all.

The successional dynamics of many hardwood stands are also linked to understory conifer patterns. These stands are usually dominated by *Alnus rubra* (red alder), which has an maximum life span of approximately 100 years (Harrington et al. 1994). Many *A. rubra* stands that established after fires 80 to 120 years ago are now experiencing high rates of overstory mortality and may senesce completely within the next few decades. Where shade tolerant conifers are present in the understory, they will be released to grow into the overstory as overstory hardwoods die. If enough understory conifers are present, the hardwood patch will eventually succeed to a conifer-dominated patch. In hardwood patches where shade-tolerant regeneration is absent, competitive clonal shrubs such as salmonberry may restrict the establishment of new tree seedlings and create a persistent shrub-dominated patch (Henderson 1978, Carlton 1988, Tappeiner 1991).

Knowing the spatial pattern of tree regeneration across a landscape would enhance our ability to identify areas where development of multilayered, late-successional structure might be limited by low abundance of understory conifers. This spatial information is currently unavailable because measurements of understory vegetation are usually taken in small field plots that are dispersed across the landscape. If forest understory characteristics are correlated with environmental or vegetation variables for which spatial data is available, however, it may be possible to use these variables to interpolate between the isolated plots – the "predictive vegetation mapping" approach reviewed by Franklin (1995). In this method, spatially referenced field plots are overlaid onto gridded maps of predictor variables in a Geographic Information System (GIS). A set of GIS variables is thereby associated with each

field plot, and these are used as independent variables to develop statistical models predicting the vegetation variables obtained from the ground plots. The statistical models are then applied to the GIS maps to predict vegetation patterns across the entire landscape.

The species niche concept provides the fundamental ecological basis for developing spatial models of regeneration patterns. Each species is assumed to occupy a realized niche space that encompasses its range of tolerance to various environmental factors such as light, moisture, and temperature while taking into account its interactions with other species (Hutchinson 1957). Our particular interest is in the regeneration niche (Grubb 1977), defined as the range of environmental conditions within which a plant species can successfully reproduce. The regeneration niche is often much narrower than the range of conditions tolerated by adults, especially in the case of trees where there is a large size disparity between seedlings and mature individuals. If we can estimate a species' regeneration niche based on field data, we may then be able to predict its spatial distribution using maps of environmental variables or their correlates. Digital elevation models, for example, can be used to derive estimates of soil moisture (Beven and Kirby 1979) and solar radiation (Bonan 1989, Nikolov and Zeller 1992), as well as slope, aspect, and other topographic indices. These types of mapped environmental variables have been used to predict landscape patterns of individual plant species (Sperduto and Congalton 1996, Baker and Weisberg 1997, Iverson et al. 1997, Guisan et al. 1998) and plant communities (Frank 1988, Davis and Goetz 1990, Lees and Ritman 1991, Brown 1994, van de Rijt et al. 1996)

When understory species or communities are being modeled, the influence of overstory vegetation on the forest floor environment must also be considered. Overstory trees can utilize large portions of available light and moisture, thereby limiting resource availability in the understory (Christy 1986). Consequently, the abundance of understory seedlings and

saplings is often sensitive to variation in overstory structure (Maguire and Forman 1983, Collins and Good 1987, Russell-Smith 1996, Schweiger and Sterba 1997, Schrader 1998) and can be particularly high in canopy gaps (Gray and Spies 1996). GIS maps of overstory tree size, canopy cover, and species composition provide some information about conditions in the forest understory and can be derived from Landsat satellite images. Spectral data from Landsat images can also be used to infer the age and successional stage of forest patches (Cohen and Spies 1992, Cohen et al. 1995).

Because plants are sessile organisms, most studies of plant species distribution have focused on relationships with local environmental conditions. In some cases, however, a species may not regenerate in a suitable habitat if seed sources are not present within the species dispersal range (Clark et al. 1998). Aerial photographs can be used to map the landscape patterns of some tree species (Mladenoff et al. 1993, Frelich and Reich 1995), but this type of mapping may not be feasible if different species have similar crown characteristics or if a species occurs mostly in the forest understory. It may be possible, however, to use other landscape attributes as indicators of potential seed source areas. In landscapes of mixed forest age classes, for example, old-growth patches represent areas that have either escaped past fires or burned at lower severity than the rest of the landscape. If these patches can be identified using aerial photographs or remote sensing imagery, they may serve as indicators of refugia for disturbance-sensitive species. In areas where fire severity is linked to landscape physiography, topographic variables might also be used to predict patterns of late-successional refugia (Camp et al. 1995).

Tsuga heterophylla (western hemlock) and *Picea sitchensis* (Sitka spruce) are the two most common understory tree species in coastal Oregon forests. *T. heterophylla* can establish under closed forest canopies (Harmon 1987) and can survive for decades in suppressed form

until it is released by canopy gap formation (Spies et al. 1990). *P. sitchensis* is less shade-tolerant than *T. heterophylla*, requiring higher light levels for establishment (Harmon 1987) and larger gaps to reach the forest canopy (Taylor 1990). Germination and early survival of both species are greater on wood substrates than on the forest floor (Harmon and Franklin 1989). Competition from mosses, herbs, and shrubs can reduce the establishment, growth, and survival of understory conifers (Harmon and Franklin 1989, Tappeiner et al. 1991). In many areas of the Coast Range, understory establishment of shade-tolerant conifers is limited by low densities of mature, seed-bearing conspecifics in the overstory (Schrader 1998). Regeneration patterns also vary regionally with climate, particularly for *P. sitchensis* which is restricted to a narrow zone of coastal fog influence (Franklin and Dyrness 1988).

Our objectives were to develop statistical models to predict the presence/absence and abundance of *P. sitchensis* and *T. heterophylla* advance regeneration using predictor variables available in GIS format, and to use these models to develop maps of regeneration patterns across the landscape. Although the predictive vegetation mapping approach has been used successfully to map individual species and plant communities in a number of ecosystems (Frank 1988, Davis and Goetz 1990, Lees and Ritman 1991, Brown 1994, Sperduto and Congalton 1996, van de Rijt et al. 1996, Baker and Weisberg 1997, Iverson et al. 1997, Guisan et al. 1998), it has not been widely applied to predicting patterns of regeneration in the forest understory (but see Baker and Weisberg 1997). We wanted to assess how much of the variability in advance regeneration density could be explained using physiographic variables derived from digital elevation models and stream maps and overstory vegetation variables derived from Landsat TM images and aerial photographs. We also wanted to determine which of these variables were most effective at predicting patterns of *P. sitchensis* and *T. heterophylla* advance regeneration.

Study Area

The Cummins Creek Wilderness, located on the Oregon Coast ten km south of Yachats, encompasses nearly 4,000 ha and includes the majority of the Cummins Creek, Little Cummins Creek, and Bob Creek watersheds. The main stems of these watersheds flow in an east to west direction, emptying directly into the Pacific Ocean. The area is mostly underlain by Yachats basalt, rather than the Tyee sandstone that dominates most of the central Coast Range. Differential weathering has produced deeply dissected terrain with long steep streams. Soils are mostly well drained Andisols and Inceptisols, and the wide valley floors of Cummins and Bob Creeks are composed mainly of alluvial sediments.

The study area falls partly within the Sitka spruce zone (Franklin and Dyrness 1988) with its eastern portion transitioning in the western hemlock zone. As a whole, the area experiences the maritime climate typical of the Pacific Northwest. Winters are mild and wet while summers are relatively cool and dry, with less than 80% of the annual precipitation falling during the growing season (Lassoie et al. 1985). Low-lying fog is common near the coast, and may extend several kilometers inland along river valleys (Franklin and Dyrness 1988). Common tree species include *P. sitchensis*, *T. heterophylla*, *Pseudotsuga menziesi* (Douglas-fir) and *A. rubra*. *Thuja plicata* (western redcedar) and *Acer macrophyllum* (bigleaf maple) are less common but still are present throughout much of the landscape.

The Cummins Creek wilderness was burned by a series of catastrophic wildfires during the late 19th and early 20th centuries, creating a mosaic of 80-120 year old stands. Old-growth trees that survived these fires are relatively uncommon and concentrated in a few remnant patches. Frequent floods have produced a finer-scale patchwork of conifers and hardwoods on the valley floors. Windthrow is common along the ridges, although large blowdown patches are rare. Both insects (bark beetle and spruce tip weevil) and disease (root

rot and hemlock mistletoe) are present in the study area, but they are not believed to have a major impact on these forests (Siuslaw National Forest 1995). Less than 5% of the study area has been cut, mostly around its perimeters; these harvested areas were excluded from the present study.

Methods

Field Data Collection

We collected forest understory data from 105 field sites during the summers of 1997 and 1998 (Figure 3.1). In 1997 we sampled intensively at 72 sites selected using a stratified random design. We divided the landscape into two geographic zones (< 5 km from the coast and > 5 km from the coast) and five topographic zones (high-order riparian areas, low-order riparian areas, lower hillslopes, middle hillslopes, and upper hillslopes). Hillslopes were then further subdivided into two aspect zones (north and south aspects). We created a map of these zones using a GIS (geographic information system) and randomly selected 4 sites in each of 12 hillslope strata (2 geographic zones x 3 topographic zones x 2 aspect zones) and 6 sites in each of 4 riparian strata (2 geographic zones x 2 topographic zones). In 1998, we sampled 33 additional sites concentrated in several geographic areas that had been undersampled by our 1997 design. These site locations were chosen subjectively using topographic maps. We decided to use this selection method for the 1998 samples because it allowed us to choose sites spanning the range of topographic strata mentioned above while also considering efficient travel paths through the wilderness. Although these sites did not comprise a truly random sample, they were not overtly biased because we did not take vegetation characteristics into account when selecting their locations.

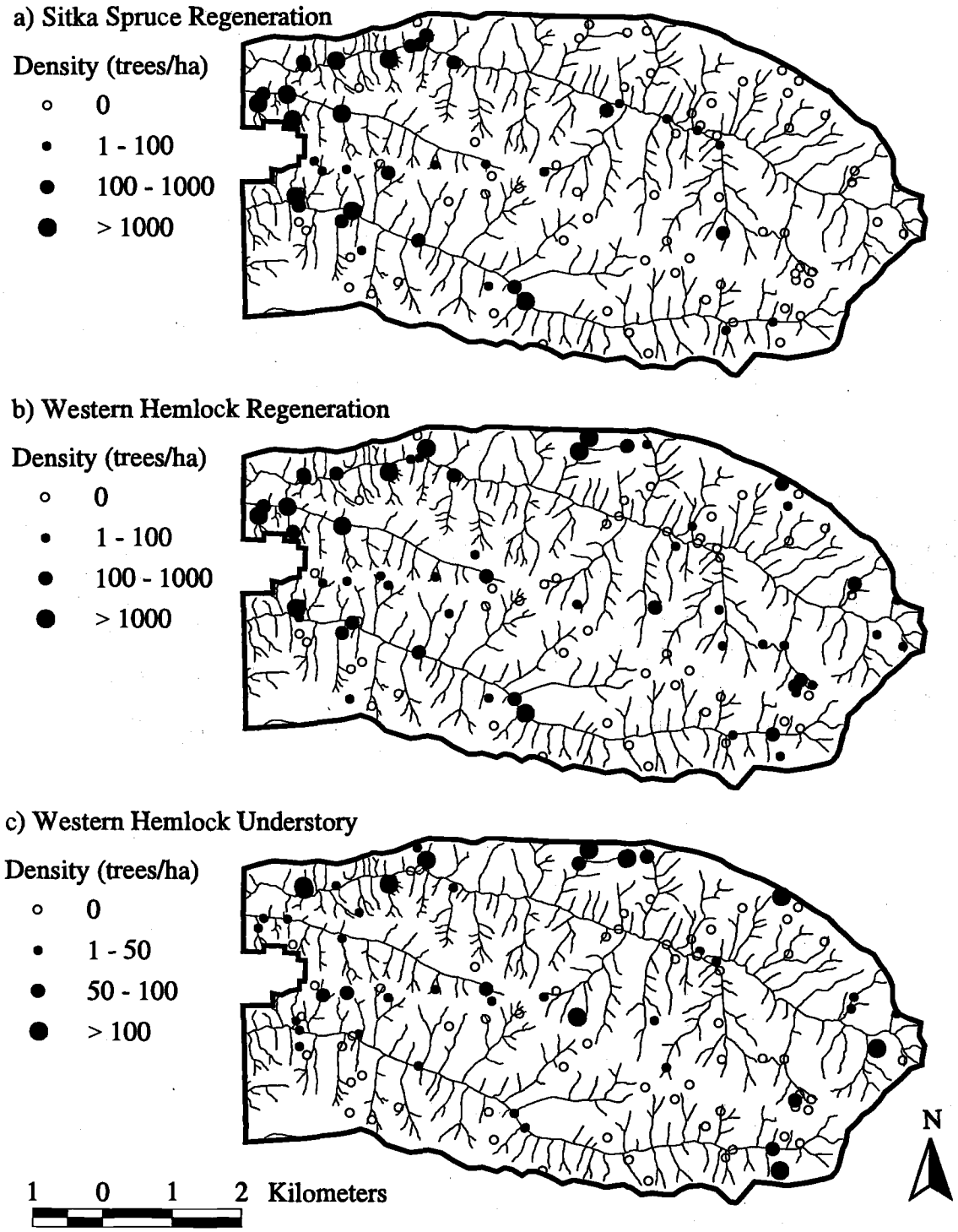


Figure 3.1: Map of field site locations in the Cummins Creek Wilderness. Symbols reflect the sampled densities per hectare of a) *P. sitchensis regeneration*, b) *T. heterophylla* regeneration, and c) *T. heterophylla* understory trees.

We located the sample sites in the field using topographic and vegetation maps. After finding the approximate location of each hillslope site, we established the center at a random distance and offset to reduce observer bias in site selection. We established the center of each riparian site on the valley floor at a random location between the stream channel and the constraining footslope. Valley floors were typically narrow in the first and second order streams (< 10 m in width) so the low-order riparian sites mostly encompassed the adjacent footslopes. Most of the high-order riparian sites were located entirely on the broad valley floors of the third and fourth order streams (20 – 140 meters in width), although some also overlapped the adjacent footslope.

Each sample site encompassed an area of approximately 0.25 ha, and included three systematically located sets of nested circular plots. In 1997, we took a set of detailed vegetation measurements at each of the 72 sites. We measured live trees (≥ 5 cm dbh) and snags (≥ 10 cm dbh and > 2 m height) in 333 m^2 plots. We recorded dbh and species of live trees and dbh and decay class of snags. Each live tree was also classified as either overstory (< 50 % of crown length beneath the level of the main canopy) or understory (≥ 50% of crown length beneath the level of the main canopy). We tallied advance regeneration (≥ 10 cm height and < 5 cm dbh) by species in 167m^2 plots. We estimated percent litter cover, percent soil cover, and percentage of vegetation browsed in 20 m^2 plots using a set of seven cover classes that approximated an arc sine–square root transformation of the percent cover data (Muir and McCune 1987). Within each set of plots, we measured down wood volume along a 20 m transect using the line intercept method. We measured percent high shrub cover (≥ 1.5 m height) at three points along each transect using a moosehorn. Plot measurements were slope-corrected and then aggregated to the site level. We obtained increment cores from several dominant, shade-intolerant trees at each site and determined tree ages by counting annual

rings under a dissecting microscope. When cores did not reach the pith we estimated tree age by extrapolating to the estimated pith locations based on the width of the oldest growth rings. Stand age was assumed to be the age of the oldest tree at each site that had established after 1850. In 1997, we only sampled understory trees and advance regeneration densities by species at the additional 33 sites.

All sample sites were georeferenced using a Trimble Pathfinder Pro XR GPS (global positioning system). A minimum of 25 3-dimensional position fixes was obtained for each sample site. Position fixes were taken with a minimum satellite elevation angle of 15 degrees, minimum signal to noise ratio of six and a maximum PDOP (position dilution of precision of six. Plot locations were differentially corrected using data from the United States Forest Service base station in Portland, OR.

GIS Data Layers

The locations of sample sites were converted into a GIS point data layer. Site locations were then overlaid on a series of grid layers to obtain a set of predictor variables for each sample site (Table 3.1). Elevation and slope were computed using a U.S. Geological Survey 30 m digital elevation model. We computed a slope curvature index in Arc/Info Grid to distinguish convex landforms (high index values) from concave landforms (low index values). Slope position was computed using an algorithm that interpolated between valley bottoms and ridges – values ranged from 0 (valley bottoms) to 100 (ridgetops). Total solar radiation input during the growing season (May-September) was calculated using the SolarImg program (Harmon and Marks 1995). Weather data to parameterize this model were taken from the nearest weather station in Newport, Oregon. Topographic moisture index (Beven and Kirkby 1979) was calculated as a function of drainage area and slope. Soil

Table 3.1: Potential explanatory variables used to develop predictive models for understory conifer patterns.

Variable	Description	Data Source
ELEVATION	Elevation above sea level (m).	Digital Elevation Model
SLOPE	Slope angle (percent slope).	Digital Elevation Model
SLOPEPOSITION	Ranges from 0 (valley bottoms) to 100 (ridgetops).	Digital Elevation Model
CURVATURE	Slope curvature (negative values are concave, positive values are convex).	Digital Elevation Model
SOLAR	Total solar radiation input during the growing season (cal cm^{-2} day^{-1}).	Digital Elevation Model
TOPOMOIST	Topographic moisture index (high values reflect greater soil moisture potential).	Digital Elevation Model
COASTDISTANCE	Distance from the coast (m).	Digital Elevation Model
RIPARIAN	Indicator variable for riparian areas.	Stream Layer
LORIPARIAN	Indicator variable for low-order (1st and 2nd order) riparian areas.	Stream Layer
HORIPARIAN	Indicator variable for high-order (3rd and 4th order) riparian areas.	Stream Layer
STREAMDISTANCE	Distance from nearest stream (m).	Stream Layer
%HARDWOOD	Percent hardwood cover.	1988 Landsat Imagery
%CONIFER	Percent conifer cover.	1988 Landsat Imagery
CROWNDIAMETER	Overstory conifer crown diameter (m).	1988 Landsat Imagery
OPENAREA	Indicator variables for areas with < 70% total overstory cover.	1988 Landsat Imagery
REMNANT	Indicator variable for old-growth remnant patches.	Aerial Photographs
REMDIST	Distance from nearest old-growth remnant patch.	Aerial Photographs

transmissivity was not included in this computation as reliable values were not available for the entire watershed. We also used the digital elevation model to determine the approximate location of the coastline and computed distance from each site to the coastline in Arc/Info Grid. Stream data came from a detailed GIS layer provided by the Siuslaw National Forest (Figure 3.2). We used the stream layer to compute stream order (Strahler 1952) and classified streams as either high-order (third and fourth order) or low-order (first and second order). The stream layer was converted to a 30 m grid for overlay with the topographic and vegetation layers. Distance from each site to the nearest stream was computed in Arc/Info Grid.

Overstory vegetation variables were derived from a 25 m resolution 1988 Landsat TM image using methodologies developed by Cohen and Spies (1992) and Cohen et al. (in press). These variables included percent conifer cover, percent hardwood cover (Figure 3.2), diameter of visible conifer crowns, and an indicator value for open areas (< 70% total overstory cover). Although there was a ten-year lag between image acquisition and ground data collection, we assumed the 1988 remote sensing layers would provide an adequate representation of the current landscape given the slow process of succession in Pacific Northwest forests and the absence of major disturbance events within the past decade. A comparison of the vegetation layers with 1995 aerial photographs supported these assumptions, indicating that landscape patterns in 1995 were similar to those in 1988. Since the size of our ground plots (0.25 ha) was larger than the individual Landsat pixels (0.0625 ha) we smoothed the vegetation layers by taking the mean values from a 3 x 3 pixel (0.56 ha) moving window. This smoothing also helped to reduce sensitivity to potential errors in the vegetation layers and in the location of the ground plots. We resampled the vegetation layers to a grid cell size of 30 m to match the resolution of the digital elevation models.

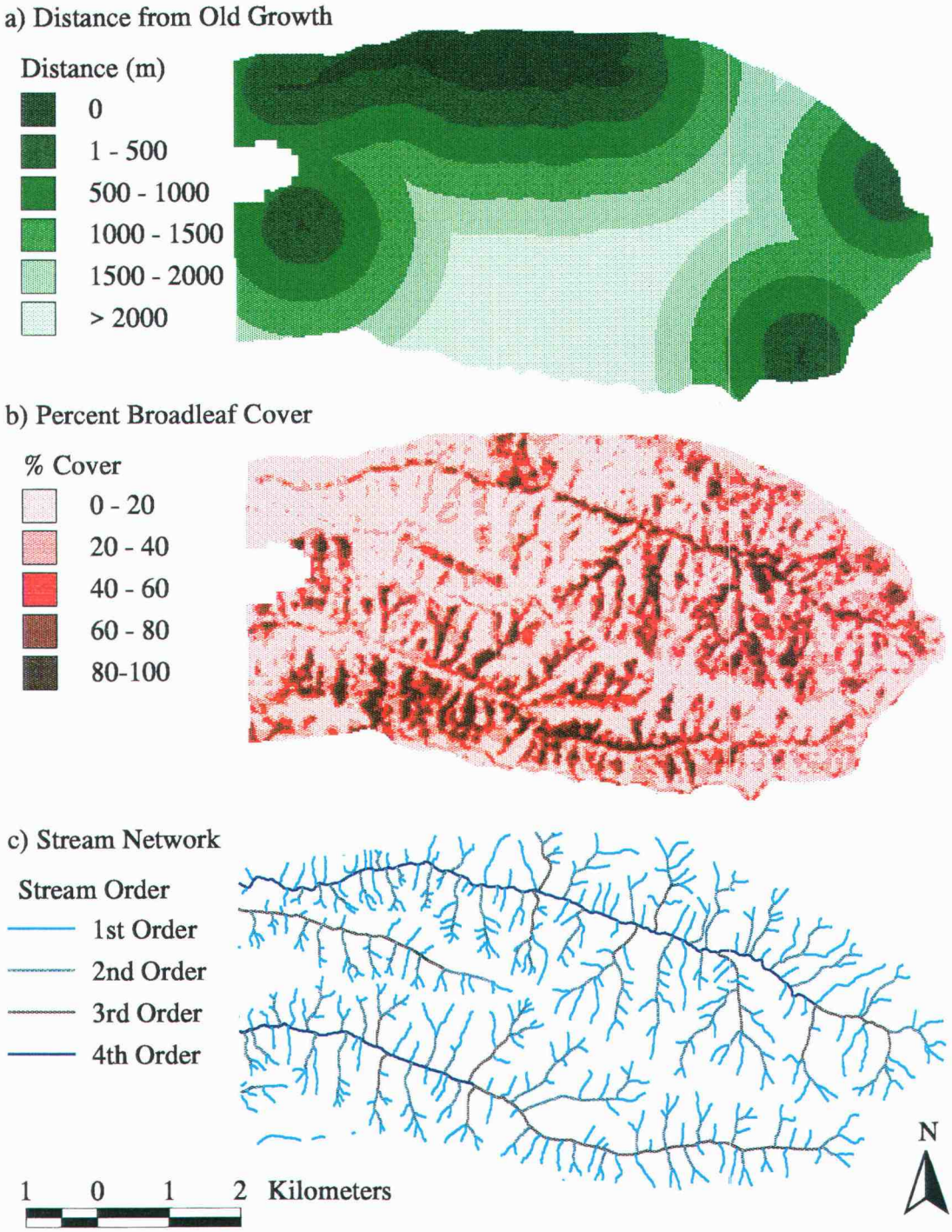


Figure 3.2: Maps of independent variables used to develop the predictive maps, including a) distance from remnant old-growth patches, b) percent broadleaf cover and c) the riparian network.

Old-growth remnant patches could not be accurately identified using the satellite imagery because many old-growth trees had broken tops and were intermixed with smaller trees. We were able to locate four remnant old-growth patches (patches containing trees that survived the 1850 fire) using 1:12,000 scale 1995 color aerial photographs viewed through a mirror stereoscope. Areas were classified as remnant patches if they were estimated to have three or more remnant trees per hectare. Individual remnant trees were not mapped because they could not be accurately identified using the aerial photographs. Old-growth patch boundaries were delimited using acetate overlays on 1:25,000 scale orthophotos. These boundaries were verified in the field at several locations. The patch maps were digitized and converted to 30 m raster data layers, and the distance of each site from the nearest remnant patch was computed using Arc/Info Grid (Figure 3.2).

Predictive Models

We developed separate statistical models for *T. heterophylla* advance regeneration, *T. heterophylla* understory trees, and *P. sitchensis* advance regeneration. *P. sitchensis* understory trees were presently only in a small portion of our sample (< 20% of the sites), and we did not attempt to model them. Since these variables all had high proportions of zero values (45-63%) we used a two-phase modeling approach (Hamilton and Brickell 1983, Guisan et al. 1998). First, binomial generalized linear models were used to predict presence/absence of each dependent variable. For sites where the value of the dependent variable was greater than zero, standard least-squares linear regression with a log-transformed dependent variable was used to predict density. The two-phase modeling approach avoided statistical problems associated with using data with a high proportion of zeroes in classical least-squares or Poisson regression. The two-phase approach also allowed for the possibility that a different set of

factors might control the presence of a particular understory species as opposed to its abundance.

Our goals in model building were to develop equations that predicted a high proportion of the variance in the dependent variable, had low multicollinearity in the predictor variables, and exhibited biologically meaningful relationships between predictor and response variables. Backward stepwise regression was used to help reduce the initial pool of predictor variables to a more parsimonious subset. Interactions between dependent variables were also explored where they were deemed to be biologically meaningful. All of the coefficients in the final models were statistically significant at the $p < 0.05$ level.

The final models were applied to maps of the independent variables to generate maps of predicted understory conifer patterns. The binary generalized linear models were used to predict locations where the understory variables were greater than zero, using the proportion of presence values in the data set as a cutoff point (Neter et al. 1989). The linear regression models were then used to predict understory density for sites where understory variables were predicted to be greater than zero.

We also generated a second set of maps incorporating the random error components of the statistical models. Instead of using a fixed cutoff to predict presence/absence, we generated an independent U(0,1) random variable for each site and considered understory conifers to be present where this random variable was less than the probability of occurrence predicted by the logistic regression equation. We used the linear regression equations to predict abundance at sites where conifers were present and incorporated variability in the predicted values by using the equation

$$Y = \exp\left(b_0 + \sum_{i=1}^{n} b_i x_i + N(MSE) \right)$$

where Y equals the predicted abundance within a given cell, b_i represents the parameters, x_i represents the independent variables, N is a standard normal random variable, and MSE is the mean squared error of the regression equation. These maps allowed us to assess the degree to which the variability unexplained by our models affected our ability to interpret the predicted patterns.

Correlation with Stand Variables

The selection of potential independent variables for the predictive models was limited by the requirement that these data be available as GIS layers. We hypothesized that in many cases these landscape variables would serve as surrogates for finer scale variables that had a more direct impact on regeneration. In order to gain a better understanding of the proximal factors influencing regeneration, we examined Pearson product-moment correlations between landscape variables that were included in the final models and a number of stand composition and structure variables computed from field data. Variation in stand structure and composition variables across three landform classes (hillslopes, low-order riparian areas, and high-order riparian areas) was also evaluated using one-way analysis of variance. Where the overall *F*-test was statistically significant, multiple comparisons were obtained using Tukey's studentized range test. Where necessary, we transformed the data using root and logarithmic functions in order to meet the assumptions of the statistical tests.

These analyses included only the 72 sites sampled in 1997 because these were the only sites where we obtained detailed measurements of stand structure. Field measurements of *P. sitchensis* and *T. heterophylla* basal area served as indicators of seed availability. Crown competition factor (Krajicek et al. 1961) provided an index of canopy closure. Percent hardwood basal area reflected differences in stand structure and understory environment in

hardwood versus conifer-dominated stands, while shrub cover reflected the influence of competing vegetation in the understory layer. Litter cover, soil cover, and down wood volume provided measures of the types and amounts of regeneration substrates available. Browse intensity, measured as the percentage of vegetation browsed, indicated the degree to which herbivory might have influenced tree seedlings and competing vegetation. Overstory age served as an indicator of successional trends since the last stand-replacing disturbance.

Results

The probability of *P. sitchensis* regeneration presence decreased with distance from the coast and was greater on lower hillslopes than on upper hillslopes (Table 3.2, Figure 3.3). *P. sitchensis* regeneration density was higher in riparian areas than on hillslopes, and decreased with distance from the coast (Table 3.3). Differences between riparian and hillslope regeneration densities were greatest near the coast, and decreased with distance inland (Figure 3.4) as expressed by the interaction term. The statistical models fit the data reasonably well; the presence/absence model had a prediction error of 0.18, while the density model had a 0.56 R^2 value. The predictive maps showed *P. sitchensis* occurring only in riparian areas and on lower hillslopes, with predicted abundance in these areas decreased with distance inland (Figure 3.5). The abrupt termination of the *P. sitchensis* distribution approximately seven km inland reflected the fixed cutoff value used to predict regeneration presence.

The probability of *T. heterophylla* regeneration presence increased with overstory crown diameter and decreased with percent hardwood cover, slope angle, and distance from remnant patches (Table 3.2, Figure 3.6). Density of *T. heterophylla* regeneration was higher than average in low-order riparian areas and lower than average in high-order riparian areas (Table 3.3, Figure 3.7). In the low-order riparian areas, *T. heterophylla* regeneration density

Table 3.2: Binary generalized linear models used to predict presence/absence of understory conifers. R^2 was computed using the method outlined by Nagelkerke (1991). % Error is the percentage of observations incorrectly classified using the proportion of presence values in the data set as a cutoff.

Model	R^2	% Error	Variable	Coefficient	p-value
P. sitchensis Regeneration	0.54	0.18	Intercept	3.605	< 0.001
			COASTDISTANCE	- 0.000553	< 0.001
			SLOPEPOSITION	- 0.0416	< 0.001
T. heterophylla Regeneration	0.24	0.33	Intercept	1.791	0.049
			%HARDWOOD$^{1/2}$	- 0.0226	0.044
			CROWNDIAMETER	0.0212	0.023
			SLOPE	- 0.0254	0.042
			REMDIST$^{1/2}$	-0.0355	0.025
T. heterophylla Understory	0.21	0.30	Intercept	2.132	0.002
			%HARDWOOD$^{1/2}$	- 0.241	0.025
			REMDIST$^{1/2}$	- 0.0448	0.004

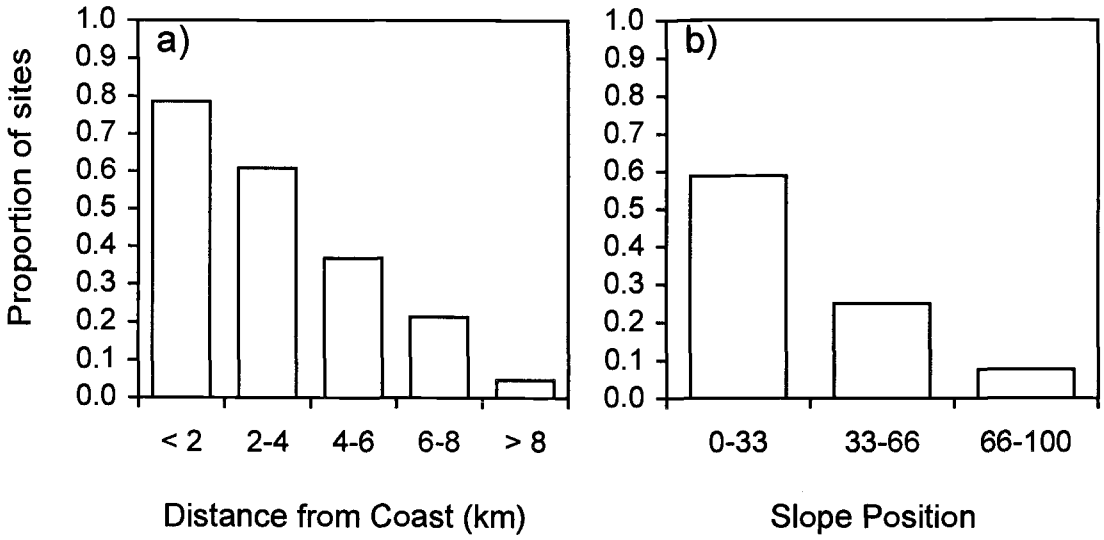


Figure 3.3: Proportion of sites with *P. sitchensis* regeneration as a function of a) distance from the coast and b) slope position.

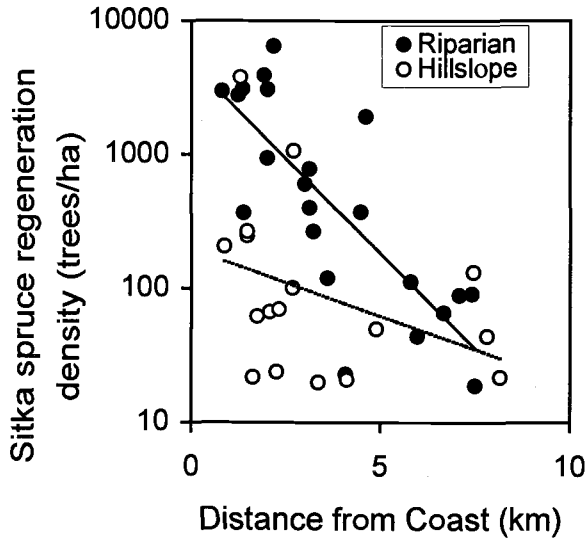


Figure 3.4: *P. sitchensis* regeneration density as a function of distance from the coast for riparian areas versus hillslopes. Lines represent least-squares regression fits.

Table 3.3: Linear regression models used to predict density (trees/ha) of understory conifers at the sites where they were present. All dependent variables were natural log transformed.

Model	R^2	Variable	Coefficient	p-value
Sitka Spruce Regeneration	0.56	Intercept	5.274	< 0.001
		RIPARIAN	3.200	0.090
		COASTDISTANCE	- 0.000228	< 0.001
		RIPARIAN x COASTDISTANCE	- 0.000425	0.025
Western Hemlock Regeneration	0.35	Intercept	5.866	< 0.001
		SLOPEPOSITION	- 0.0194	0.006
		HORIPARIAN	- 1.1871	0.045
		LORIPARIAN	2.030	0.016
		COASTDISTANCE	- 0.0000277	0.693
		LORIPARIAN x COASTDISTANCE	- 0.000376	0.030
Western Hemlock Understory	0.22	Intercept	3.584	< 0.001
		$\%HARDWOOD^{1/2}$	0.180	0.047
		HORIPARIAN	- 1.014	0.028
		$REMDIST^{1/2}$	- 0.0203	0.033

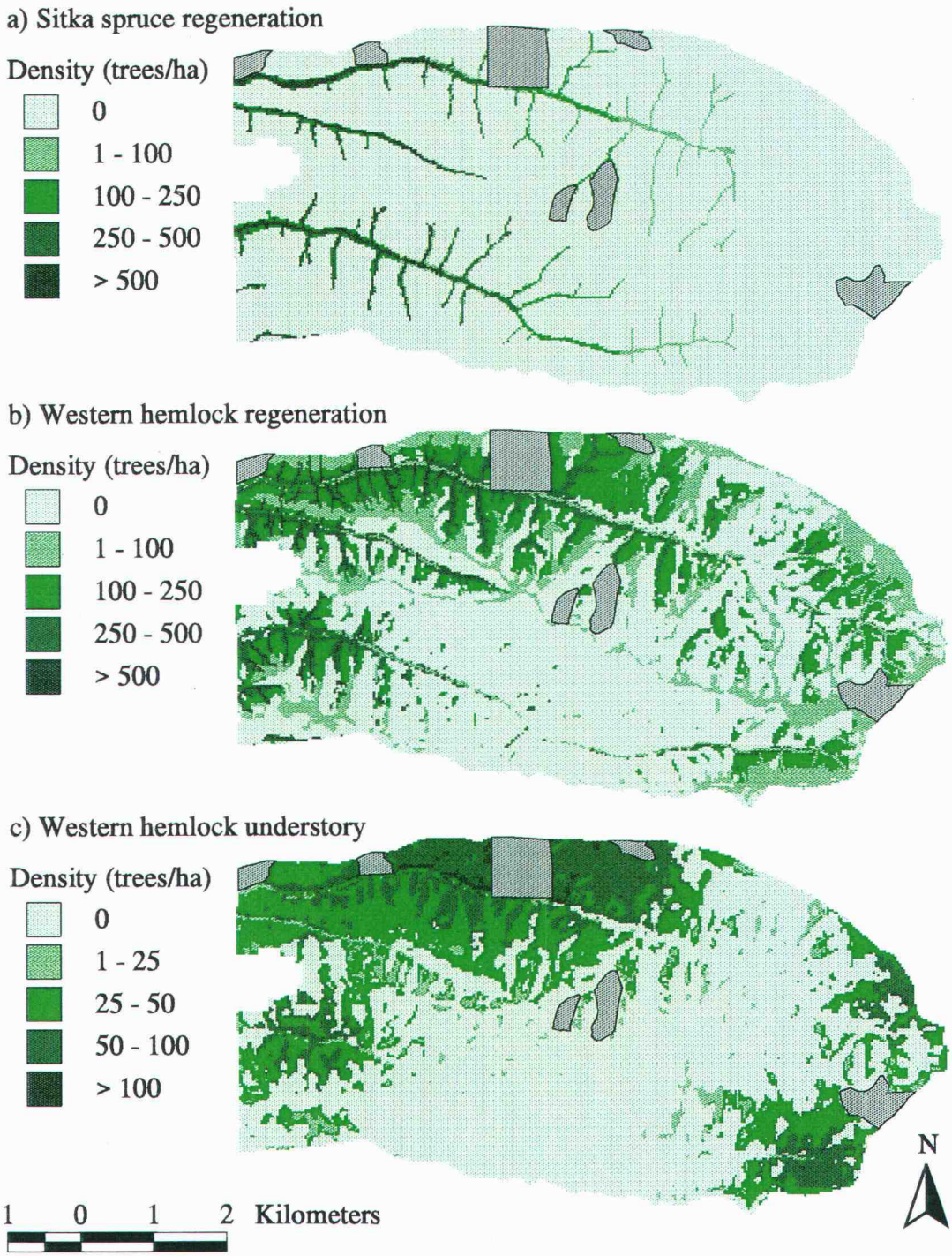


Figure 3.5: Maps of predicted conifer patterns generated using a fixed cutoff to predict presence/absence and the mean regression response to predict density. a) *P. sitchensis* advance regeneration, b) *T. heterophylla* advance regeneration and c) *T. heterophylla* understory trees. Individual grid cells are 30 x 30 m (0.09 ha) in size. Shaded areas represent cut stands that were excluded from our analysis.

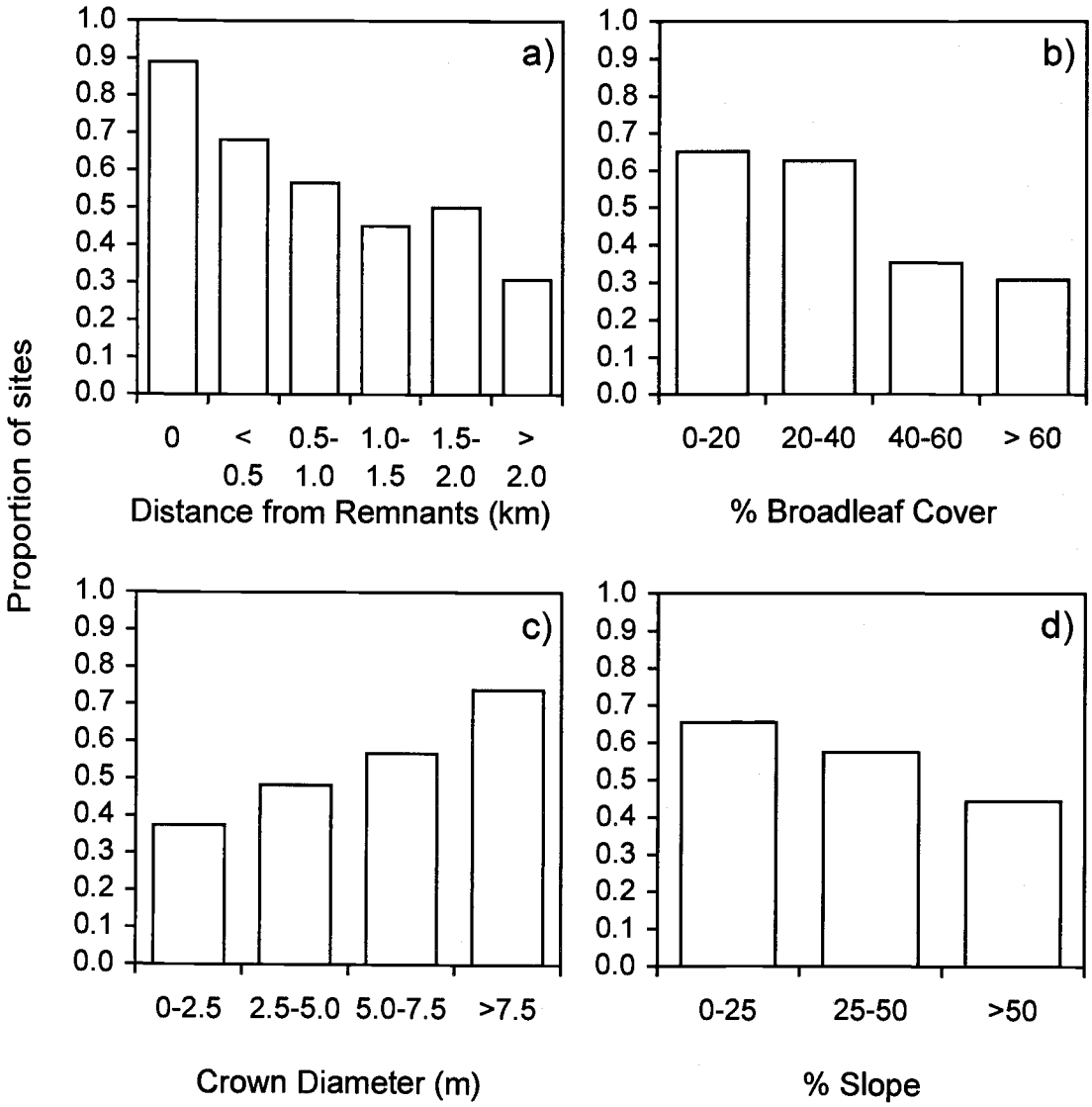


Figure 3.6: Proportion of sites with *T. heterophylla* regeneration as a function of a) distance from the nearest old-growth remnant patch, b) percent broadleaf cover, c) overstory conifer crown diameter and d) percent slope.

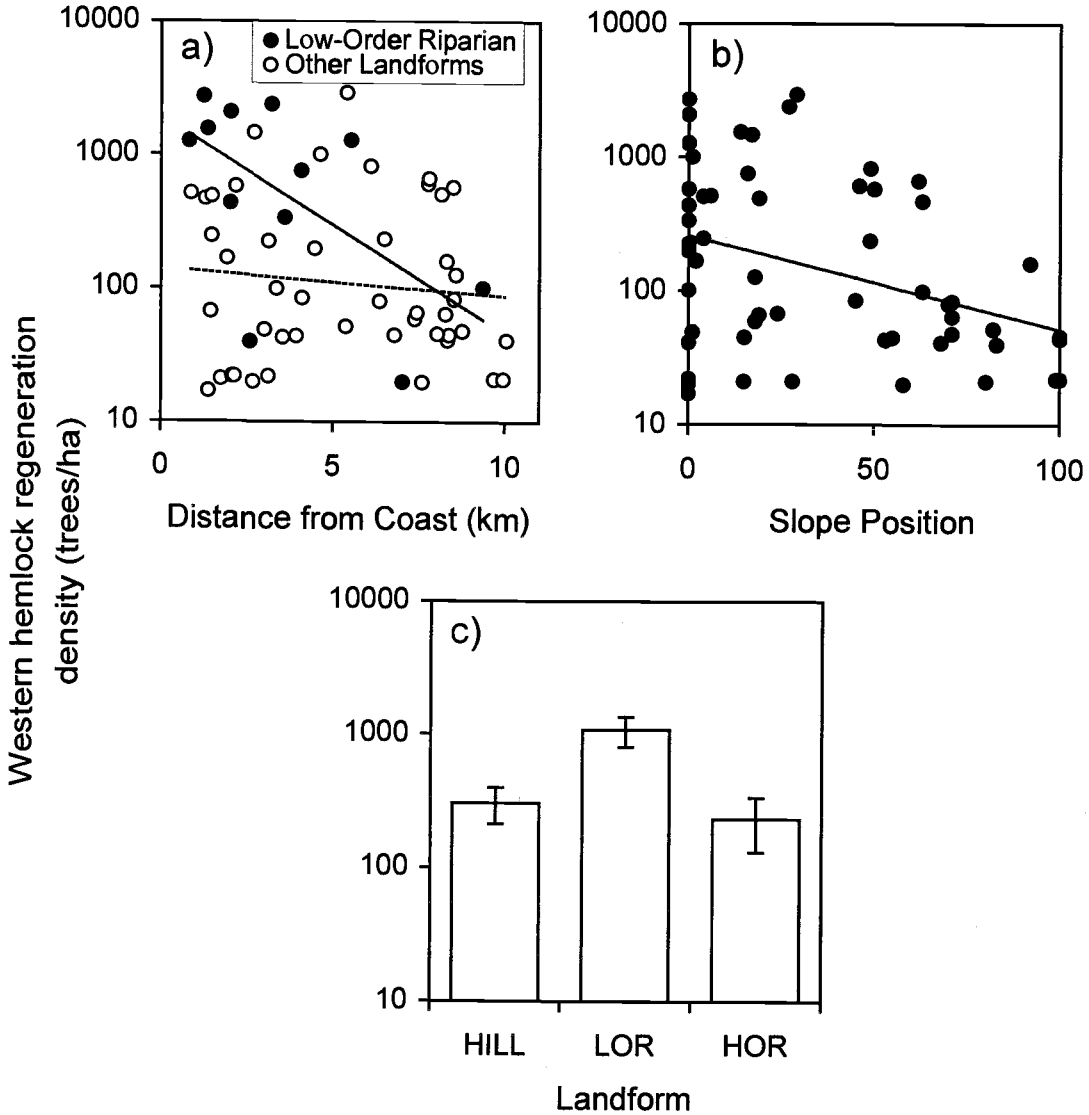


Figure 3.7: *T. heterophylla* advance regeneration density as a function of a) distance from the coast for low-order riparian areas versus other landform types, b) slope position and c) landform where HILL=hillslopes, LOR=low-order riparian areas, and HOR=high-order riparain areas. Lines are least-squares regression fits. Error bars represent standard errors.

decreased with distance from the coast. *T. heterophylla* regeneration density also decreased with hillslope position. These models did not fit the data as well as the *P. sitchensis* regeneration models; the presence/absence model had a prediction error of 0.33, while the density model had a 0.35 R^2 value. The mapped distribution of *T. heterophylla* regeneration revealed large-scale patterns related to the locations of remnant old-growth patches, as well as finer-scale patterns reflecting variation in overstory vegetation and topography (Figure 3.5). Predicted density was highest in riparian areas close to the coast.

The probability of *T. heterophylla* understory tree presence decreased with increasing hardwood cover and distance from remnant patches (Table 3.2, Figure 3.8). Potential abundance increased with hardwood cover, decreased with distance from remnant patches, and was lower in high-order riparian areas than on other landforms (Table 3.3, Figure 3.9). Although the plot of understory tree abundance versus hardwood cover did not suggest a strong relationship, the response was more pronounced once the effects of distance from remnant patches and high-order riparian areas were also considered. The presence/absence model for *T. heterophylla* understory trees had a prediction error of 0.30, while the density had a 0.22 R^2 value. The mapped distribution predicted that both the occurrence and abundance of *T. heterophylla* understory trees were highest in and around old-growth remnant patches (Figure 3.5).

When we included statistical error in the map of *P. sitchensis* regeneration (Figure 3.10), the predicted distribution appeared generally similar to the map based on fixed cutoff values and mean responses (Figure 3.5). Regeneration was still confined to riparian areas and lower hillslopes, and the trend in decreasing abundance with distance from the coast was still discernible. Fine-scale variability in *P. sitchensis* abundance was more evident, however, and the predicted range extended further inland than in the map generated using a fixed cutoff for

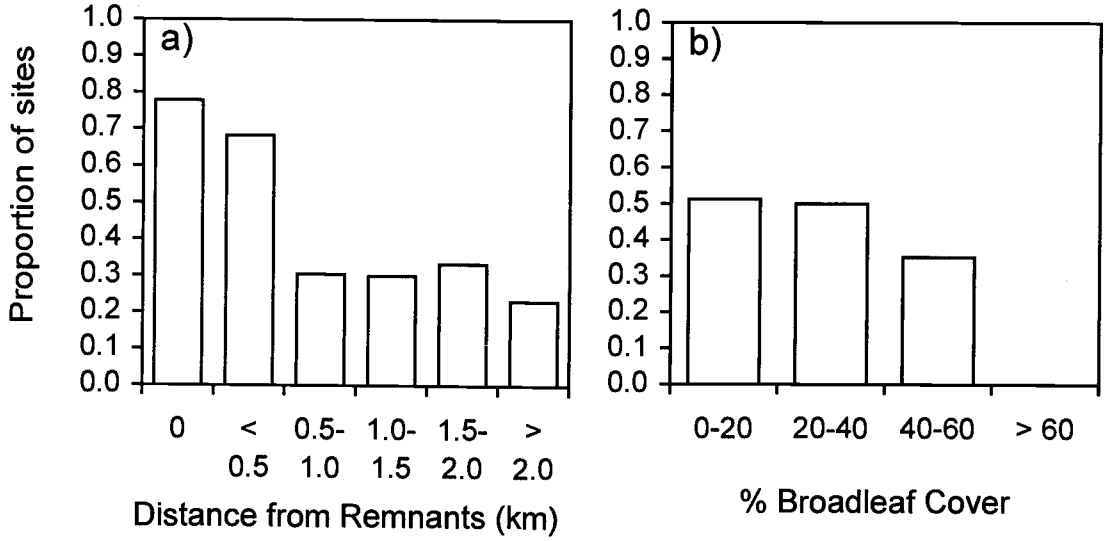


Figure 3.8: Percentage of sites with understory *T. heterophylla* trees as a function of a) distance from remnants and b) percent broadleaf cover.

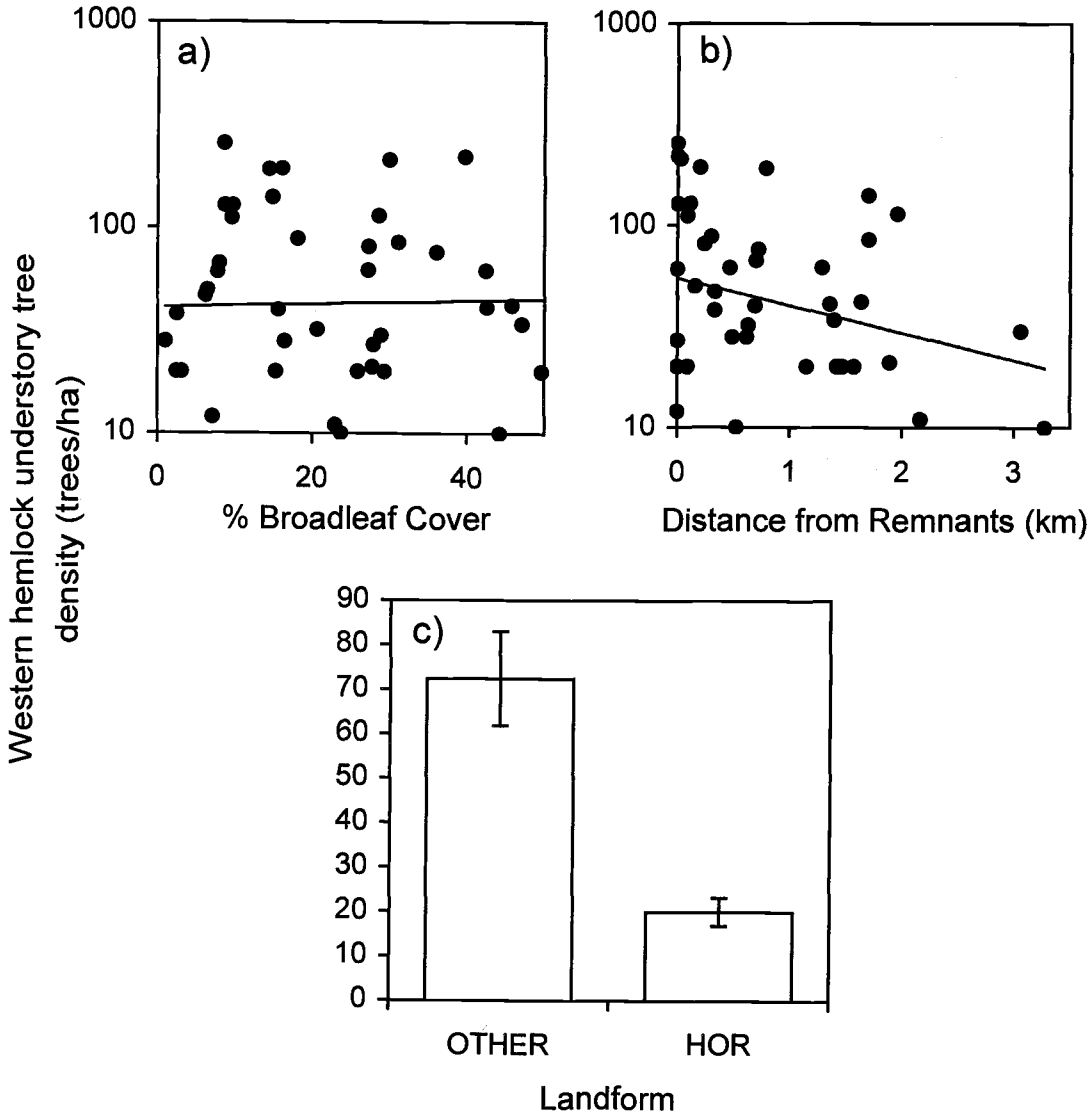


Figure 3.9: *T. heterophylla* advance regeneration density as a function of a) percent broadleaf cover, b) distance from old-growth remnant patches and c) landform where HOR=high-order riparian areas and OTHER=other landform types. Lines are least-squares regression fits. Error bars represent standard errors.

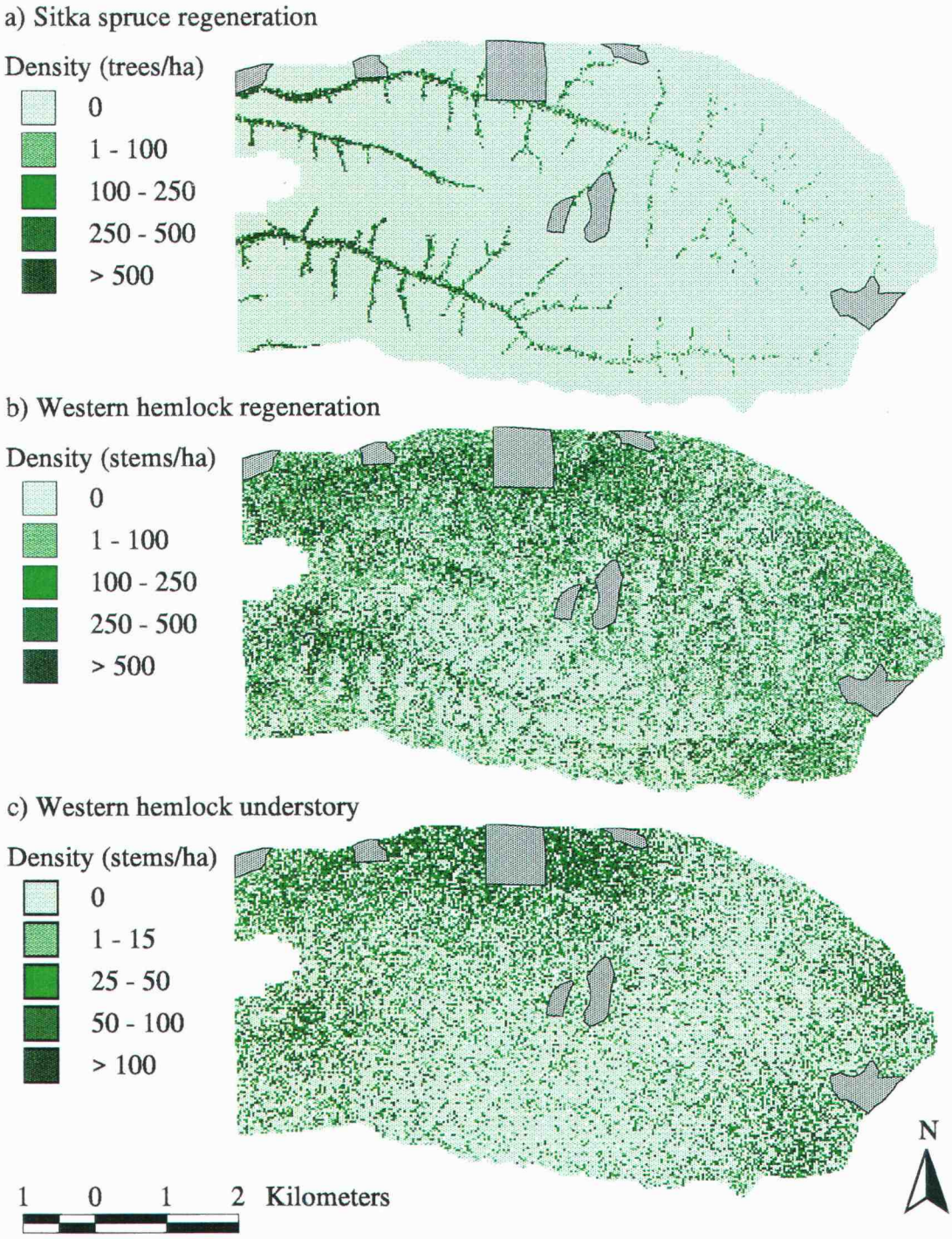


Figure 3.10: Maps of predicted conifer patterns generated using probabilistic predictions of presence/absence and incorporating random error into the prediction of density. a) *P. sitchensis* advance regeneration, b) *T. heterophylla* advance regeneration c) *T. heterophylla* understory trees. Individual grid cells are 30 x 30 m (0.09 ha) in size. Shaded areas represent cut stands that were excluded from our analysis.

presence/absence. Incorporating the random error terms had a much greater effect on the predictions of *T. heterophylla* regeneration and understory tree patterns than on *P. sitchensis* (Figure 3.10). Although large-scale trends related to the patterns of old-growth patches were still discernible, random errors obscured much of the finer-scale pattern related to topography and overstory vegetation.

Distance from the coast had a strong negative correlation with *P. sitchensis* basal area and a weaker negative correlation with *T. heterophylla* basal area (Table 3.4). Slope was negatively correlated with down wood volume. Slope position was correlated with a number of stand variables; hardwood basal area, shrub cover, soil cover, down wood volume, and overstory age were all highest at lower slope positions, while crown competition factor was highest at upper slope positions. Percent hardwood cover was also correlated with many of the stand variables; *T. heterophylla* basal area, *P. sitchensis* basal area, and crown competition factor were negatively correlated with percent hardwood cover, while hardwood basal area,shrub cover, soil cover, and browse intensity were positively correlated with percent hardwood cover. Visible crown diameter was negatively correlated with crown competition factor, and positively correlated with hardwood basal area, soil cover, down wood volume, and stand age. Basal area of both *T. heterophylla* and *P. sitchensis* decreased with distance from old-growth remnants, while browse intensity increased with distance from old-growth remnants. Riparian sites had higher stand ages and down wood volumes than hillslope sites and lower crown competition factors than hillslope sites (Table 3.5). High-order riparian sites had higher hardwood basal area, higher browse intensity, and lower litter cover than low-order riparian areas and hillslopes. Low-order riparian areas had higher shrub cover and soil cover than other parts of the landscape.

Table 3.4: Pearson product-monent correlation between GIS variables used in the predictive models and stand attributes measured in the field plots. Only the 72 plots sampled in 1997 were included in this analysis.

	GIS Variables					
Stand variables	Distance from coast	Slope angle	Slope position	Percent hardwood cover	Visible crown diameter	Distance from old growth
T. heterophylla basal area	–0.37**	–0.01	–0.20	–0.27	0.07	–0.49**
P. sitchensis basal area	–0.74**	–0.14	–0.21	–0.24	0.09	–0.35**
Crown competition factor	0.05	0.20	0.48**	–0.37**	–0.34**	–0.09
% hardwood basal area	0.10	–0.16	–0.34**	0.71**	0.31**	0.22
Percent canopy gaps	0.24	0.01	–0.07	0.09	0.22	–0.03
Percent high shrub cover	0.18*	–0.01	–0.32**	0.41**	0.14	0.13
Litter cover	–0.19	0.18	0.06	–0.22	–0.01	–0.16
Exposed soil	0.03	0.02	–0.38**	0.40**	0.37**	0.15
Browse intensity	0.04	–0.05	–0.06	0.25*	0.16	0.28**
Down wood volume	0.08	–0.31**	–0.41**	0.12	0.27**	–0.21
Overstory age	0.09	–0.16	–0.57**	0.23	0.34**	0.15

* $p < 0.05$
** $p < 0.01$

Table 3.5: Mean values of stand attributes measured in the field plots for each of three landscape categories used in the predictive models. Standard errors are given in parentheses. Values with different letters were significantly different at the $p < 0.05$ level based on multiple comparisons using Tukey's studentized range test. Only the 72 plots sampled in 1997 were included in this analysis.

	Landscape Unit		
Stand variables	High-order riparian area (n=14)	Low-order riparian area (n=18)	Hillslope (n=74)
P. sitchensis basal area (m^2/ha)	14.8 (6.4)	9.0 (3.3)	11.1 (3.6)
T. heterophylla basal area (m^2/ha)	3.2 (1.8)	8.9 (4.2)	5.2 (1.2)
Crown competition factor	116.6a (18.4)	133.5a (16.2)	226.6b (9.5)
Percent hardwood basal area	51.5a (10.8)	21.0b (5.5)	13.2b (3.0)
Percent high shrub cover	18.8ab (18.8)	34.8a (5.7)	14.3b (2.6)
Percent canopy gaps	21.0 (8.0)	25.7 (5.1)	18.4 (2.2)
Litter cover (Indexed from 1-7)	3.6a (0.2)	4.2ab (0.2)	4.5b (0.2)
Exposed soil (Indexed from 1-7)	2.6ab (0.2)	2.7a (0.1)	2.1b (0.1)
Browse intensity (Indexed from 1-7)	3.6a (0.4)	2.2b (0.3)	2.6b (0.2)
Down wood volume (m^3/ha)	1566.6a (389.7)	1848.8a (295.6)	747.8b (142.1)
Overstory age (years)	116.0a (4.4)	114.8a (3.9)	99.2b (2.6)

Discussion

Validity of the Modeling Approach

Although we found statistically significant relationships between understory variables and the mapped explanatory variables, our models explained only low to moderate amounts of the variation in the dependent variables. Like most predictions made using statistical models, the maps in Figure 3.5 ignore the random error that is associated with each response. Although these maps illustrate detailed spatial patterns of presence/absence and abundance, they only reflect trends related to the portion of variation in the response that is explained by the statistical models. If the models explain only a small portion of the total variation, these maps will tend to imply a lower amount of variability than is present in the real landscape.

This problem becomes evident when maps generated using fixed cutoff points to predict presence/absence and mean responses to predict abundance (Figure 3.5) are compared with maps generated from the same models, but with random errors incorporated into the predictions (Figure 3.10). In the case of *P. sitchensis* regeneration, the statistical models explain more than half of the variation in presence/absence and density and the two maps are quite similar. In contrast, the *T. heterophylla* models account for much less variability in the response variables and the predicted patterns change more drastically once the error terms are introduced. When the presence/absence *of T. heterophylla* regeneration is predicted using a fixed cutoff, for example, the model predicts a large patch void of regeneration in the central and southern portion of the study area (Figure 3.5). When probabilistic predictions are used, however, the map instead predicts a frequency gradient ranging from high frequencies in and around old-growth patches to low frequencies in large hardwood patches and in areas far from old growth (Figure 3.10). Our field observations suggest that the probabilistic map is more

representative of the patterns that actually occur on the landscape–*T. heterophylla* regeneration is never completely absent from large portions of the landscape, nor does it occur at uniformly high density in others.

Much of the unexplained error in our models arises from the coarse nature of our predictor variables. Seedling establishment and survival is known to be associated with many microsite-scale factors such as environmental suitability (Harmon 1987, Christy 1986), substrate availability (Harmon and Franklin 1989, Gray and Spies 1996), and competition with other plants (Maguire and Forman 1983, Harmon and Franklin 1989). Our choice of predictor variables was limited, however, by the requirement that they be available in mapped format. Although our environmental indices reflected relative environmental variation with distance from the coast and physiography, they could not predict finer-scale microenvironmental patterns that can have a strong influence on seedling populations. Similarly, although our remote sensing derived estimates of overstory vegetation were correlated with a number of stand-level there was still a large amount of structural variability that could not be predicted from these measures. Even if we were able to obtain more detailed measurement of the seedling habitat at each site, it is still unlikely that we could ever predict all of the variation in the responses. Other less predictable factors such as inter-annual variability in the size of seed crops (Pickford 1929) and short-term climate fluctuations (Baker 1990) limit our ability to predict the occurrence and abundance of regeneration based on habitat alone.

Given these difficulties, it is unlikely that it will ever be possible to develop very precise predictions of seedling patterns based on GIS variables. Even so, predictive vegetation mapping can still provide valuable insight into large-scale vegetation patterns and the underlying ecological factors that influence them. One of the great advantages of this method

is that the georeferenced field inventory data, digital elevation models, and remote sensing maps needed to make these kinds of predictions are readily available in many areas. Predictive maps of advance regeneration and other vegetation attributes can potentially provide valuable information for use in management and conservation as long as they are interpreted cautiously. In most cases, it is probably more reasonable to interpret the mapped patterns as qualitative trends rather than precise, quantitative predictions.

Remnants and the Role of Disturbance

Biological legacies, such as remnant old-growth trees, are known to influence the pathways and rates of forest succession in individual stands (Swanson and Franklin 1992). Our results showed a larger-scale relationship between understory *T. heterophylla* and remnant old-growth patches, on the order of hundreds to thousands of meters. These old-growth patches were found on both north and south aspects, at topographic positions ranging from riparian areas to upper hillslopes, and at a range of distances from the coast. Because of the wide range of physiographic and climatic settings where the remnant patches were found, it is unlikely that their relationship with *T. heterophylla* regeneration is a spurious association reflecting some underlying environmental gradient (Chapter 2). Instead, we hypothesize that this spatial association reflects the higher availability of *T. heterophylla* seed in and around the remnant patches, as evidenced by the negative correlation of distance from remnant patches with *T. heterophylla* basal area.

The remnant old-growth patches that we identified using aerial photographs were comprised mostly of old-growth *P. menzeisii*. We also found several old-growth *T. heterophylla* in the large patch in the northwest section of the study area, and in the smaller patch in the southeast corner. The thin bark, shallow rooting habit, and relatively flammable

foliage of *T. heterophylla* make it extremely fire-sensitive (Minore 1979, Agee 1993). We reasoned that the current locations of old-growth remnant patches represent areas where historical fire severity was lower than in other portions of the landscape, and where *T. heterophylla* therefore had a higher probability of surviving fires and dispersing seeds. In comparison, individual old-growth *P. menziesii* were scattered more broadly across the landscape, suggesting that seed sources for this fire-tolerant species were more widely distributed. Of course, the old-growth trees found on the landscape today do not represent all of the seed sources present following the historical disturbances. Some trees are damaged but not killed outright and may survive long enough to disperse seeds, only to succumb within a few years to pathogens and disease (Franklin et al. 1987).

We hypothesize that more *T. heterophylla* survived the fires long enough to disperse seeds in and around the old-growth patches than in other portions of the landscape. The density of *T. heterophylla* seed dispersed into forest openings drops rapidly within several hundred meters from the source (Pickford 1929, Issac 1930, Gashwiller 1969). Therefore, higher seed availability may account for the higher basal areas of *T. heterophylla* currently found near old-growth patches. In addition, shading from remnant trees probably favored establishment of the shade-tolerant *T. heterophylla* in and directly adjacent to the remnant patches. Some of these trees may have survived for a hundred years or more in suppressed form (Schrader 1998) and now comprise a portion of the understory *T. heterophylla* population. Trees that established after the fires also provide the seed sources for most of the *T. heterophylla* advance regeneration currently found in the forest understory. Because seed dispersal distances for *T. heterophylla* beneath closed canopies are very low, on the order of tens of meters (Schrader 1998), the current pattern of advance regeneration is still tightly linked to the overstory patterns that established following the historical fires.

T. heterophylla regeneration also occurred more frequently at sites with larger overstory conifer crown diameters than at sites with smaller overstory trees. This trend may reflect structural changes that occur with increasing stand age such as larger tree sizes, decreasing canopy cover, and increases in down wood volume (Spies and Franklin 1991). If this is the case, younger stands that currently have small overstory trees, dense canopies, and low levels of down wood may gradually develop these stand attributes over time. If maps such as ours are used to predict where multilayered forest canopies will develop in the future, they will need to account for successional changes that will occur in the young stands and possibly increase suitability for understory regeneration over time.

Riparian Areas

Regeneration patterns in riparian and hillslope sites exhibited different responses to the coast-to-inland climatic gradient. *P. sitchensis* and *T. heterophylla* regeneration in riparian areas increased sharply with proximity to the coast, while regeneration density on hillslopes exhibited a comparatively weak response. The high regeneration densities predicted along coastal streams contradict previous findings that conifer regeneration in relatively uncommon in Central Coast Range riparian areas (Minore and Weatherly 1994, Hibbs and Giordano 1996, Pabst and Spies in press), and suggest that the coastal riparian areas have environmental and structural features particularly suited for the establishment and survival of conifer seedlings.

Several factors may account for the high abundance of tree regeneration in coastal riparian areas. The first is the coastal fog zone, which extends further inland along river valleys than on hillslopes (Franklin and Dyrness 1988). Both *P. sitchensis* and *T. heterophylla* seedlings are intolerant of moisture stress (Minore 1972), and low-lying fog during the dry

summer months both reduces evaporative demand and contributes precipitation in the form of fog drip (Franklin and Dyrness 1988). Different forest structures in riparian areas compared to hillslopes may also contribute to the higher regeneration densities in coastal riparian forests. The importance of down wood as a regeneration substrate for both *P. sitchensis* and *T. heterophylla* has been well established (Harmon and Franklin 1989, Gray and Spies 1996) and the high volume of down wood in riparian areas may provide more opportunities for establishment than on hillslopes. The open-canopy riparian forests allow more light to reach the forest floor, while heavy browsing by deer and elk in high-order riparian areas may reduce shrub competition. Because *P. sitchensis* regeneration is less tolerant of shade than *T. heterophylla*, the low light levels beneath the dense hillslope forests are probably another factor limiting its distribution to the open riparian areas.

The lower than average density of *T. heterophylla* regeneration along high-order streams, in contrast with higher than average density in low-order coastal riparian areas, is difficult to explain. Higher *T. heterophylla* seed availability in the low-order riparian areas than in high-order riparian areas may partially account for this pattern (Table 3.5). *T. heterophylla* may also be more heavily browsed in the high-order riparian areas than *P. sitchensis*. Our results should caution scientists and managers against automatically assuming that advance regeneration observed in riparian areas will be similar to those observed on the adjacent hillslopes. These results also demonstrate that vegetation in riparian areas and hillslopes may exhibit different responses to geographic variation in climate.

Fate of Hardwood Patches

Most of the hardwood-dominated hillslope stands within the Cummins Creek Wilderness lack *T. heterophylla* in their understories. Of our 30 sample sites with greater than

40 percent hardwood cover, only 20 percent had understory western hemlock trees and 33 percent had western hemlock regeneration. The decreasing probability of *T. heterophylla* presence with increasing hardwood cover probably reflects the low volumes of down wood, low basal areas of *T. heterophylla* seed sources, and high shrub densities found in hardwood-dominated stands (Henderson 1978, Carlton 1988). Because of high *P. sitchensis* regeneration in many riparian areas near the coast, some of the hardwood patches along coastal streams may develop into conifer stands as the hardwood overstory senesces. The surrounding conifer matrix may subsume relatively small hardwood patches as adjacent tree crowns expand into the area formerly occupied by hardwoods. It seems unlikely, however, that most large hardwood patches in riparian areas farther from the coast and on hillslopes will have sufficient advance regeneration to succeed to conifer stands over the next several decades.

Although *T. heterophylla* understory trees were rarely found in patches with high hardwood cover, their density actually increased slightly with increasing hardwood cover. It may be that in situations where *T. heterophylla* can establish either on down logs or in gaps in the shrub layer, higher light levels under mixed hardwood/conifer canopies might lead to increased growth and survival. This change in sign for a variable in the abundance model compared to the presence/absence models is an excellent illustration of a type of relationship that cannot be captured by a single-equation model, but is easily expressed in the two-phase modeling approach.

There are two possible ways to interpret the apparent tendency for hardwood succession to shrubs on the current landscape. One hypothesis is that these shrub patches are an artifact of anthropogenically-driven increase in fire frequencies during the late 19th and early 20th centuries (Impara 1997, Weisberg 1998). These fires may have led to mass movement that favored establishment of alder on the mineral soil and also reduced the

abundance of shade-tolerant, fire-sensitive species such as western hemlock. This idea is supported by our observations of large remnant conifer stumps from the previous stand in many patches that are currently hardwood-dominated, which suggest that the total area of conifer-dominated forest may have been greater than in the past. If this scenario is true, then management activities such as shrub removal and replanting with conifers might be appropriate in some situations to increase the amount of conifers on the landscape.

An alternative interpretation, however, is that shrub-dominated patches are a natural part of an ecosystem where aggressive, clonal shrubs can effectively compete with trees in the understory layer. From this perspective, shrub-dominated patches can be viewed as integral components of late-successional landscapes that may have important ecological functions. As an example we observed heavy levels of use by elk and deer in many open, shrub dominated areas of the landscape, as evidenced by high levels of browse damage and high densities of scat and trails. Conifer regeneration in these patches might eventually occur if browsing by ungulates reduces shrub competition or if fallen trees from neighboring conifer patches open up gaps in the shrub layer. Although several studies have explored the ecology and dynamics of transient canopy gaps in Pacific Northwest forests (Spies et al. 1990, Taylor 1990), little work has been done on the ecology of persistent canopy gaps. More research will be necessary before deciding what approaches to take to managing this vegetation type.

Conclusions

We found a number of statistically significant and biologically meaningful relationships between understory conifers and predictor variables derived from satellite remote sensing, aerial photographs, digital elevation models, and stream maps. The models only accounted for small to moderate amounts of the variability in understory conifer patterns,

however. While the predicted maps provide a useful qualitative illustration of landscape patterns, they should not be expected to predict understory conifer density at a given point with high precision. As in previous predictive vegetation mapping studies, we found that advance regeneration patterns were correlated with environmental variables derived from digital elevation models and overstory vegetation measurements made with Landsat TM satellite images. We also found that advance regeneration in riparian area exhibited stronger responses to climatic gradients than advance regeneration on hillslopes. Unlike previous efforts, we found that a map of spatial proximity to remnant old-growth patches was also correlated with advance regeneration patterns and improved our ability to develop predictive models. We suggest that predictor variables related to disturbance history and the riparian network could enhance other attempts at predictive vegetation mapping in Pacific Northwest forests.

CHAPTER 4

Modeling the Temporal and Spatial Dynamics of a Late-Successional, Fire-Sensitive Tree Species

Michael C. Wimberly and Thomas A. Spies

Abstract

Tsuga heterophylla (western hemlock), a fire-sensitive, late-successional tree species, is an important component of old-growth forest structure in the Pacific Northwest. In the Oregon Coast Range, however, *T. heterophylla* occurs at low densities or is completely absent from many conifer stands. Field data suggest that this patchy distribution may arise in part from historical fire patterns and seed dispersal limitations. We explored this hypothesis using a spatially explicit, patch-based simulation model that integrated dispersal and life-history characteristics of *T. heterophylla* with disturbance regimes operating at multiple scales. Analysis of this model showed that the amount of *T. heterophylla* on the landscape was particularly sensitive to variations in the fire return interval and fire severity. *T. heterophylla* was less sensitive to variations in post-fire remnant patch density, canopy gap return interval, probability of recruitment in canopy gaps, and the probability of "background" dispersal events that were independent of seed source distances. Brief periods of high fire frequency caused a rapid and persistent decline in the amount of *T. heterophylla* on the landscape. Short dispersal distances in closed-canopy forests, the requirement for canopy gap disturbances to facilitate overstory recruitment, and the lag time between recruitment and reproductive maturity limited the rate of *T. heterophylla* population growth during the intervals between fires. These results corroborate empirical observations that the abundance and pattern of *T. heterophylla* are sensitive to fire history, and suggest that the impacts of fire may persist for many centuries.

Introduction

Over the past two decades, considerable attention has been focused on the ecological role of old-growth forests in Pacific Northwest landscapes. In the Oregon Coast Range, fires

and logging have eliminated most of the pre-settlement old-growth forests, creating a landscape matrix dominated by relatively young forests with a few old-growth fragments (Means et al. 1996). This widespread and rapid change in landscape pattern has led to concern for the viability of native species associated with old-growth habitats. As a result, current management plans on federal lands are focused on preserving existing old growth and increasing the amount of old growth currently on the landscape (FEMAT 1993). These plans assume that forests currently in the young and mature stages have the capacity to develop the structural characteristics of old growth over the next century.

Characterizations of old growth have often emphasized its striking individual structures, such as large live trees, snags, and down logs. Equally important, however, are stand structural features such as a wide range of tree sizes, a continuous vertical distribution of foliage throughout the canopy, and a patchy, heterogeneous understory (Franklin and Spies 1991). Development of these stand-level characteristics is associated with increases in the abundance of shade-tolerant trees as the forest ages. Although *Tsuga heterophylla* (western hemlock) is generally assumed to be the dominant late-successional tree species in the Oregon Coast Range (Franklin and Dyrness 1988), field research has shown that this species actually has a very patchy distribution, particularly in the Central Coast Range. A study of unmanaged conifer stands in the Coast Range found that half of these stands studied lacked *T. heterophylla* regeneration, while 31% did not have any *T. heterophylla* in the overstory (Schrader 1998). Data from permanent inventory plots tell a similar story, with *T. heterophylla* absent at 55% of sites in the Coast Range (Janet Ohmann, unpublished data). The absence of *T. heterophylla* seed sources in many areas has generated concern that some forests may not develop the old-growth structural characteristics associated with shade-

tolerant trees within the time frames assumed in the Northwest Forest Plan, and has raised questions about the ecological factors responsible for these landscape patterns.

Ecological studies of forest community composition have traditionally focused on environmental gradients as the dominant factors controlling species distributions (Curtis and McIntosh 1951, Whittaker 1956; 1960). In the Oregon Coast Range, for example, *T. heterophylla* is more abundant in the cool, moist climates of the coastal and northern areas than in warmer and drier areas in the south and along the Willamette Valley margin (Ohmann and Spies 1998). The abundance of *T. heterophylla* and other shade-tolerant trees varies along topographic gradients as well, tending to be highest on moist sites located on north aspects or lower hillslope positions (Spies and Franklin 1991, Weisberg 1998). While continuing to recognize the role of environmental variability, current ecological theory also emphasizes the dynamic and spatially interactive nature of landscapes and the influences of spatial processes such as disturbance and dispersal on species pattern and abundance (Pickett and White 1985, Clark and Ji 1995). *T. heterophylla* is known to be extremely fire sensitive (Agee 1993, Minore 1972), suggesting that historical fires may have played a role in structuring its current distribution. For example, stands that regenerated after a single, stand-replacing burn typically have higher levels of *T. heterophylla* than stands that reburned one or more times after the initial fire (Klopsch 1985, Poage 1995, Gray and Franklin 1997). This effect has been attributed to higher mortality leading to seed source limitations in the reburned stands. Given that fire frequencies increased markedly in the Coast Range during the late 19th and early 20th centuries (Impara 1997), it is possible this type of reburning might account for the absence of *T. heterophylla* in many areas.

The main goal of this study was to explore the influences of disturbance and seed dispersal limitation on *T. heterophylla* population dynamics in a spatially explicit landscape

framework. Our overarching hypothesis was that short periods of high fire frequency can lead to sustained decreases in the landscape abundance of fire-sensitive, late-successional tree species like *T. heterophylla*. We expected that the abundance of *T. heterophylla* in a landscape would be sensitive to the frequency, severity, and pattern of fires, as well as rates of gap formation and recruitment in these gaps. Our specific objectives were to: 1) Develop a conceptual model of *T. heterophylla* population dynamics that incorporated disturbance and dispersal across multiple scales, 2) Design a computer program to simulate the basic elements of this conceptual model, 3) Assess model sensitivity to various disturbance and life-history parameters, and 4) Use the model to simulate *T. heterophylla* response to temporal variation in fire frequency.

Conceptual Framework

Forest dynamics operate through the establishment, growth, and mortality of trees over a range of spatial and temporal scales (Urban et al., 1987). Spies and Franklin (1989) proposed a simplified hierarchy that subdivides these processes into coarse and fine-scale dynamics. Coarse-scale dynamics are driven by disturbances such as fire, wind, and volcanic eruption that operate at spatial scales of 0.1 to >100,000 hectares and at temporal scales ranging from decades to millennia. The environment created by these disturbances allows *T. heterophylla* to establish along with shade-intolerant species such as *Pseudotsuga menzeisii* (Douglas-fir) and *Alnus rubra* (red alder). Coarse scale dynamics create a landscape of even-aged, relatively homogeneous forest patches, or stands. Fine scale dynamics operate within these patches, and are driven by disturbances such as wind, pathogens, and insects that result in the death of individuals or small groups of canopy trees (Spies and Franklin 1989, Taylor 1990). These fine-scale processes are important for the development of late-successional

structure; dead trees contribute to the snag and down wood resources, while resources released by the overstory facilitate the regeneration and growth of *T. heterophylla* and other shade-tolerant trees.

Wildfire was historically the dominant coarse-scale disturbance in Pacific Northwest Douglas-fir forests (Agee 1993). Fire regimes exhibited considerable regional variability. In the Central Washington Cascades, for example, the fire history of Mt. Rainier National Park was characterized by mostly high-severity fires with a natural fire rotation of more than 400 years (Hemstrom & Franklin 1982). In comparison, the drier Central Oregon Cascades, had fire rotations ranging from 95 to 149 years with a larger proportion of low severity burns (Morrison & Swanson 1990). The fire regime of the central Oregon Coast Range consisted of a mixture of high and low severity fires, with a natural fire rotation varying between 200 and 300 years over the past several millennia (Impara 1997, Long et al. 1998). *T. heterophylla* has thin bark, shallow roots, and flammable foliage, and is considered a fire-sensitive "avoider" species (Agee 1993, Minore 1972). A fire mortality model incorporating crown and bole damage predicted 99% mortality of *T. heterophylla* for a typical stand in the Northern Rocky Mountains (Peterson and Ryan 1986). Survival of *T. heterophylla* and other fire-sensitive species is often spatially restricted to patches of forest that either escape the fire entirely or burn at low severity (Camp et al. 1995).

Many forest dynamics models, including most gap dynamics simulators (Urban and Shugart 1992), assume that recruitment is independent of the forest overstory. Other models that incorporate seed dispersal, however, have demonstrated that dispersal limitations can have a strong impact on community dynamics (Green 1989, Clark and Ji 1995, Pacala and Deutschman 1995). *T. heterophylla* produces lightweight seeds that can disperse for hundreds of meters into openings created by fires or other coarse-scale disturbances. Some *T.*

heterophylla seeds released from a box kite at 60 m elevation in a 20 kph wind traveled more than 1,100 m, although only 20% of the seeds fell further than 670 m from the release point (Issac 1930). A study *of T. heterophylla* dispersal from a remnant forest edge reported similar distances, with 13% of the seeds travelling 1000 m or more (Pickford 1929).

Because *T. heterophylla* does not form a persistent seed bank (Burns and Honkala 1990) seeding establishment patterns are likely to be correlated with patterns of seed rain. Heavier seed rain leads to higher saturation of potential safe sites with propagules, and therefore higher establishment rates (Horn 1981). Decreases in seedling density with distance form seed sources have been observed in Pacific Northwest forests (Harris 1967) as well as in other temperate forest ecosystems (Johnson 1988, Myster and Pickett 1992). These patterns may persist for many years if the initial cohort continues to dominate the forest canopy. In the Cummins Creek Wilderness, where a series of catastrophic fires occurred 80-120 years ago, *T. heterophylla* basal area in the current landscape still decreases with distance from remnant old-growth patches (Chapter 2).

In the intervals between large wildfires, the disturbance regime is dominated by small canopy gaps. In the Central Oregon Cascades, most gaps are formed when trees die standing, creating canopy openings ranging from 25 m^2 to 300 m^2 in size (Spies et al. 1990). Bole breakage by wind is the primary gap-forming agent in coastal forests, creating gaps up to 850 m^2 in size (Taylor 1990). Despite their small sizes, canopy gaps occur with greater frequency than large fires, and can therefore disturb an equally large area over time (Spies and Franklin 1989). *T. heterophylla* seedlings can establish underneath a closed forest canopy and survive for a century or more in suppressed form (Schrader 1998), but typically require one or more gap disturbances to reach the forest canopy (Spies et al. 1990). When canopy gap formation does not disturb the forest floor, *T. heterophylla* advance regeneration is released from

overstory competition for light and moisture and rapidly increases growth (Oliver 1976, Alaback and Tappeiner 1991). Higher resource levels following gap formation also increase rates of seedling establishment. The density, species composition, and spatial pattern of seedlings will vary with canopy gap size, and the abundance and pattern of various microsites such as litter mineral soil, and dead wood (Gray and Spies 1996; 1997).

Recruitment of *T. heterophylla* in canopy gaps will only occur if reproductively mature individuals are close enough to either produce advance regeneration or establish new seedlings in the gap. When *T. heterophylla* establishes in open conditions following a large disturbance, dominant trees typically reach reproductive maturity within 30 years (Burns and Honkala 1990). Small, suppressed individuals produce only a small amount of cones compared to larger individuals in dominant canopy positions (Schrader 1998) and can functionally be regarded as non-reproductive juveniles. These trees will not become reproductively mature until they are released by a gap disturbance. Dispersal distances tend to be much shorter in closed canopy forests than into large openings because of slower wind speeds and physical interference from neighboring trees. In one study, for example, most *T. heterophylla* seedlings were found within 10 m of a parent tree, with a maximum distance of 18 m (Schrader 1998).

It is also likely that rare, long-distance dispersal events will occur. Although the majority of wind-dispersed seeds fall in close proximity to the seed source, their long-tailed dispersal curves suggest that high winds or other rare events can occasionally carry seeds over much longer distances (Greene and Johnson 1995). Traditional seed dispersal studies cannot detect these events, since the maximum distance sampled is usually 1,000 meters or less from the seed source. A few long-distance dispersal events can lead to increased rates of population growth because they create new dispersal foci from which *T. heterophylla* can expand into

areas of the landscape that are otherwise inaccessible to short-distance seed dispersal (Shigesada et al. 1995).

Modeling Approach

Because of the large spatial scales and long time intervals required to study landscape processes such as disturbance and dispersal, experimental and observational studies are difficult to implement. Simulation modeling provides a viable alternative for studying landscape dynamics and developing hypotheses about these complex, large-scale systems (Baker 1989). Previous research has provided us with considerable information about *T. heterophylla* establishment (Christy and Mack 1984, Harmon 1987, Harmon and Franklin 1989, Gray and Spies 1996; 1998), dispersal (Issac 1930, Pickford 1929, Schrader 1998) and response to disturbance (Peterson and Ryan 1986) that can be applied in the development of a model. There are still considerable gaps in our knowledge of *T. heterophylla* population dynamics, however, particularly with respect to the growth and mortality in the understory sapling bank.

We developed a relatively simple patch-based model driven by a small set of parameters, suitable for exploring general hypotheses about the population dynamics of *T. heterophylla* and similar fire-sensitive, late-successional species (Fahrig 1990). While this type of model does not realistically simulate all aspects of *T. heterophylla* life history, nor make accurate predictions of *T. heterophylla* abundance, it is valuable as a simple simulation tool to help us understand how processes such as disturbance and dispersal interacting spatially across multiple scales might have influenced historical and present-day patterns of *T. heterophylla*. Similar modeling approaches have proved useful for studying the influence of fire regimes on the population viability of fire-sensitive shrubs (Bradstock et al. 1995),

demonstrating how spatial interactions contribute to cyclic dynamics in European beech forests (Wissel 1992), exploring the influence of spatial factors on the coexistence of trees and grass and semiarid savannas (Jeltsch et al. 1996), and examining the influences of disturbance and dispersal on species coexistence (Green 1989).

Methods

Model Description

We used a cellular automata framework to model the spatial and temporal dynamics of *T. heterophylla* populations. Cellular automata models simulate landscapes in a discrete-space, discrete-time framework with each cell taking on one of a finite set of possible states (Wolfram 1984). In our model, we used a 100 by 100 grid of cells, each assumed to represent an area of approximately 0.25 ha (50 m x 50 m). Landscape dynamics were modeled as a series of 10-year time steps. Cells were assigned to one of four classes: 1) Cells with juvenile (non-reproductive) *T. heterophylla* present, 2) Cells with reproductively mature *T. heterophylla* present, 3) Forest matrix cells (containing no *T. heterophylla*) without canopy gaps, and 4) Forest matrix cells with one or more canopy gaps (Figure 4.1). In order to give our model more ecological realism, we had to relax some of the assumptions of classical cellular automata. In addition to the discrete cell states, we also tracked the age of *T. heterophylla* cells in order to model the transition from juvenile to reproductive states. Instead of assuming that cells interacted only with neighboring cells, we allowed spatial interactions across the entire grid in order to reflect the potential for long-distance dispersal following fires. Finally, instead of a deterministic rule set, cell transitions were based on a set of probabilistic rules and equations designed to reflect the variability and uncertainty inherent in disturbance and dispersal processes.

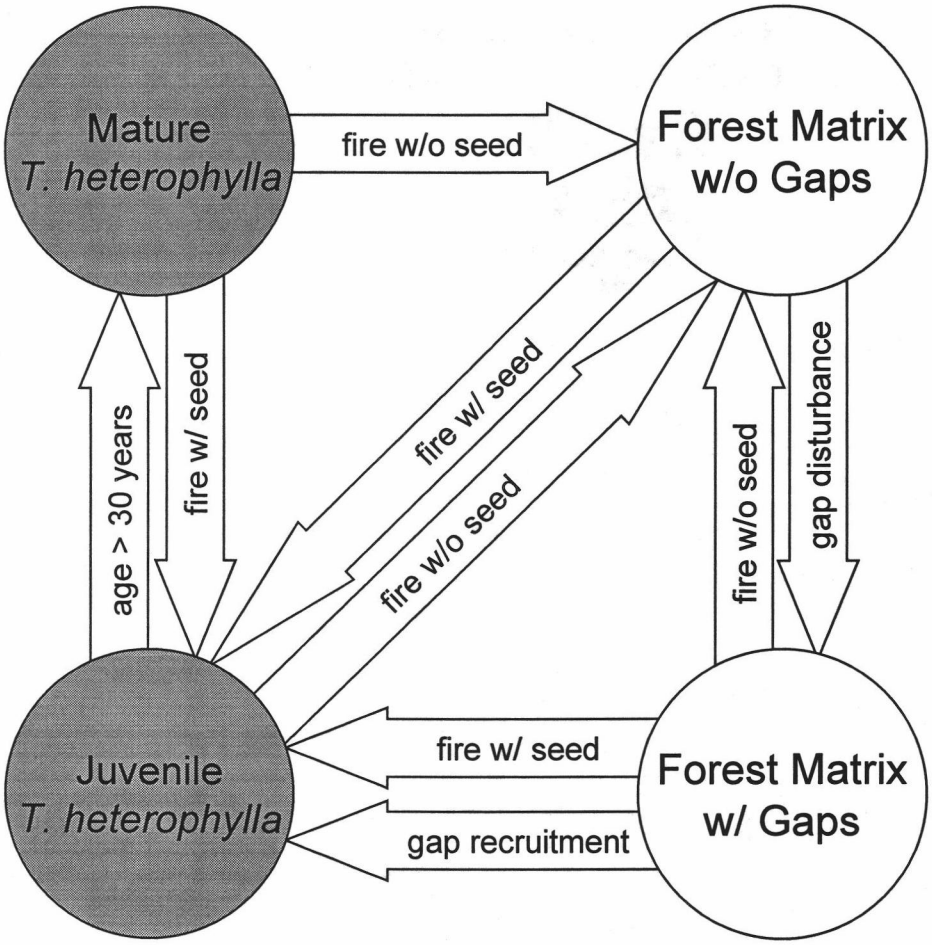


Figure 4.1: State and transition diagram for the *T. heterophylla* patch dynamics model. Circles denote the four possible states for model cells, and arrows represent the possible transitions that can occur among these states.

The age of *T. heterophylla* cells was incremented by 10 years at the beginning of each time step. Aside from the presence and absence of canopy gaps, the dynamics of forest matrix cells were not explicitly simulated. The number of fires occurring in a ten-year time step was modeled as a Poisson random variable with parameter λ computed as $\lambda = 10/\text{FRI}$, where FRI equaled the mean time between fires. Fires were assumed to burn across the entire model extent, but were modeled as mosaics of high and low-severity patches. *T. heterophylla* was assumed to survive only in low-severity patches. The proportion of the landscape burned at high severity by each fire was specified by the fire severity parameter, FSEV. The spatial heterogeneity of fires was controlled by the PATCH variable, which represented the number of low-severity patches left by each fire. The size of each low severity patch was then computed as the total area of low severity fire divided by the number of low-severity patches. These patches were centered on randomly selected cells, and their configuration was generated using a stochastic algorithm.

After a fire, *T. heterophylla* recruitment could potentially occur in all cells on the landscape. The probability of recruitment in a given cell was assumed to be a function of seed availability, and was modeled as a function of distance from seed sources. Only cells containing reproductively mature *T. heterophylla* could disperse seeds. *T. heterophylla* was assumed to reach reproductive maturity at age 30 in all our simulations (Burns and Honkala 1990). Probability of establishment was assumed to equal one at the seed source, and to decrease as a negative exponential function of distance from the seed source with parameter λ = FDISP. We chose an FDISP value of 0.005 for our simulations, generating a dispersal curve that predicts a recruitment probability of 0.78 at cells adjacent to a seed source, declines to 0.05 at 600 m from the seed sources, and approaches zero at approximately 1000 m from the seed source (Figure 4.2). Each reproductively mature *T. heterophylla* cell on the landscape

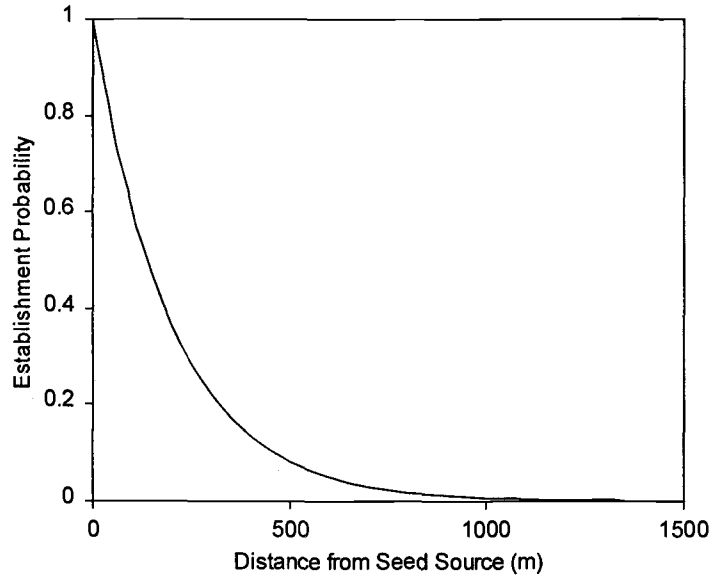


Figure 4.2: Probability of *T. heterophylla* establishment as a function of distance from seed source when FDISP=0.005.

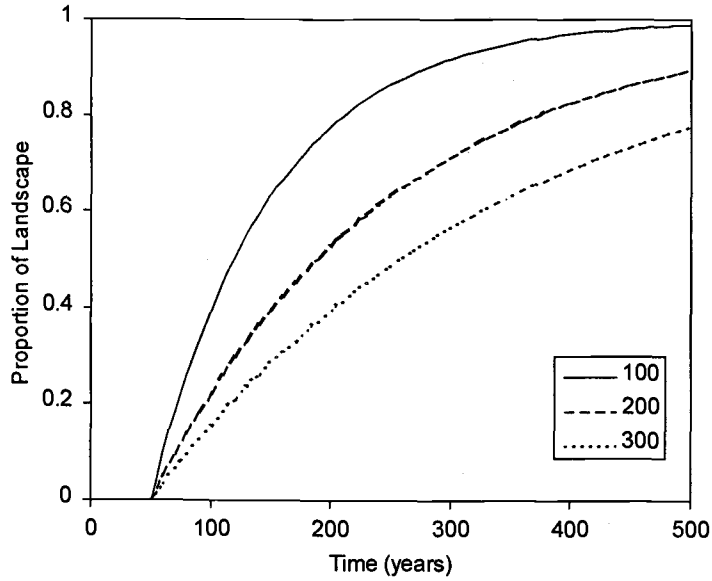


Figure 4.3: Expected cumulate proportion of the landscape with canopy gaps as a function of time since fire for three values of the gap return interval parameter (GRI).

was assumed to have an independent probability of dispersing into each unoccupied cell. We also simulated background dispersal, which was independent of the density and pattern of seed sources and allowed for the possibility of long distance dispersal events. Background dispersal was simulated independently for each cell with probability specified by the BDISP parameter. Cells where recruitment was successful were initialized as juvenile *T. heterophylla* cells at age 0. Otherwise, cells were initialized as forest matrix cells with no canopy gaps.

Canopy gaps did not occur during the first fifty years following stand initiation. This lag reflected the stem exclusion phase of stand development, when dense canopies prevent most light from reaching the forest floor (Oliver and Larson 1990). Once a forest matrix cell reached age 50, the probability of gap occurrence during each 10-year time step was computed as 10(1/GRI), where GRI equaled the mean time to gap occurrence. Model cells (0.25 ha) were larger than the size of most canopy gaps (0.0025-0.1 ha), so gap occurrence did not necessarily imply disturbance of the entire cell. Instead, it meant that one or more canopy gaps of a size suitable to allow canopy recruitment had occurred somewhere within the cell. Viewed from a stand scale, the gap formation process reflects the transition from a young, closed-canopy stands to a heterogeneous late successional stand with increasing opportunities for overstory recruitment as time progresses (Figure 4.3). Once gap disturbance occurred in a forest matrix cell, the cell remained in the gap phase until *T. heterophylla* was recruited in the cell or a fire occurred. Thus, the proportion of the landscape where overstory recruitment can occur increased asymptotically to 100% over time, with a rate that increased with decreasing GRI.

Recruitment could potentially occur in gap-phase cells if a seed source was available. Because the size of the simulation cells (50 m) was larger than the 18 m maximum understory dispersal distance measured for *T. heterophylla* (Schrader 1998), seed was assumed to only

disperse from reproductively mature *T. heterophylla* in the eight neighboring cells. Details of the recruitment processes such as the spatial pattern of microsites and the establishment, survival, and growth of individual seedlings were not simulated. A particular recruitment event could have conceivably represented either release of advance regeneration previously established in the forest understory, or the establishment of new seedlings. Each potential source cell was assumed to have an independent probability of dispersing into the destination cell, as specified by the gap recruitment parameter (GREC). Background dispersal could also occur in gap phase cells, with a probability of establishment in each time step equal to BDISP.

If establishment was successful, the gap phase cell became a juvenile *T. heterophylla* cell with age 0. Otherwise, the cell remained in the gap phase and recruitment could occur in subsequent time steps. Once *T. heterophylla* established in a cell, subsequent gap and recruitment events were not tracked; the population within the cell was assumed to be self-sustaining until fire mortality occurred.

We developed a computer program in C to link these rules and equations in a spatially explicit framework. This model could be run in one of two different modes. In the batch mode, the model could make replicate runs of a number of different parameter combinations and tally the number of cells in each class at specified intervals. The program also had a graphical mode, in which a color-coded map of the simulated landscape was displayed on the computer screen during each time step. Visualization of the model output proved particularly useful for helping us understand the basic spatial processes of the model, and for helping us to interpret the results of our sensitivity and experimental analyses.

Model Analysis

We carried out a sensitivity analysis to quantify *T. heterophylla* response to life-history and dispersal parameters. Our response variable was *T. heterophylla* landscape frequency, computed as the proportion of cells on the landscape containing either juvenile or mature *T. heterophylla.* We used a Latin hypercube sampling design (Schwatzman and Kaluzny 1987) to construct a response surface as a function of the fire return interval (FRI), fire severity (FSEV), density of remnant patches (PATCH), gap return interval (GRI), gap recruitment probability (GREC), and background dispersal probability (BDISP). Minimum and maximum values for each parameter were selected to span what we considered to be a reasonable range for Pacific Northwest forests (Table 4.1). We divided the total range of each variable into three equal sections, producing a total of 3^6=729 strata. We randomly selected one set of parameter values from each stratum, with each parameter sampled as a uniform random from the appropriate section.

We made an independent model run for each parameter set, starting from a randomly generated landscape pattern. The length of each run was four times the simulated fire frequency, which allowed time for the simulated processes to overwrite the initial landscape configuration. The final value of *T. heterophylla* landscape frequency was taken as the response value for each parameter set. We then used non-parametric, local regression models (Cleveland et al. 1993) to generate response surfaces for individual parameters and combinations of parameters. These models produced smoothed regression function that effectively displayed both linear and nonlinear response trends.

We also carried out a simulation experiment to assess temporal responses to changes in fire frequency. This experiment encompassed five scenarios, each 800 years in length. In the control scenario, FRI was set at 300 years for the entire 800 years. In the treatment

Table 4.1: Parameter values used in the model analysis. Sensitivity runs were made using a Latin hypercube design with the range of each parameter divided into three bins of equal size. Mean values from these ranges were used in the simulation experiment examining temporal variation in fire frequency. Fire frequency values are not listed for the simulation experiment, because time series of fire frequencies were defined separately for the control and treatment scenarios.

		Sensitivity Analysis		Simulation
Parameter	Description	Minimum	Maximum	Experiment
FRI	Fire return inverval (years)	100	400	N/A
FSEV	Fire severity (% of landscape burned	0.85	1.0	0.925
PATCH	Density of remnant patches	1	9	5
GRI	Gap return interval (years)	100	400	250
GREC	Probability of recruitment in canopy gaps	0.0	1.0	0.5
BDISP	Background dispersal (recruitment probability independent of seed source location)	0	0.015	0.0075

scenarios, FRI was set at 300 for the first 200 years, lowered for the next 50 years and then returned to 300 for another 550 years. We lowered FRI to values of 50, 100, 150, and 200 in the four treatment scenarios. The treatments were intended to reflect the temporal pattern of fire frequencies observed over much of the Pacific Northwest. In general, a period of relatively infrequent fires during the pre-settlement period (approximately 1500-1850) was followed by increased fire frequency during the settlement period (approximately 1850-1910). Once fire suppression came into effect during the early 20th a return to infrequent fires occurred (Weisberg 1998).

We made 100 replicate simulations of both the control and treatment runs for each of the four scenarios. Each run was initialized with a random landscape, but was allowed a 900-year burn-in period to overwrite the starting configuration. Once the burn-in period was completed, *T. heterophylla* landscape frequency was recorded at 50-year intervals. Treatment effect was summarized by subtracting the mean frequency for the control run from the mean frequency for the treatment runs and computing the 95% confidence interval for the difference in mean values (Zar 1984). The other model parameters were set at the median values from the ranges used in our sensitivity runs (Table 4.1).

Results

Graphical analysis of our model runs at various parameter settings emphasized the influences of remnant patch density fire and severity on the establishment of the post-fire *T. heterophylla* cohort. These analyses also demonstrated that the initial post-fire distribution of *T. heterophylla* left a persistent imprint on landscape patterns. For example, when fire left a single remnant patch, post-fire establishment of *T. heterophylla* was restricted to the area immediately around that remnant patch (Figure 4.4). This initial distribution expanded slowly,

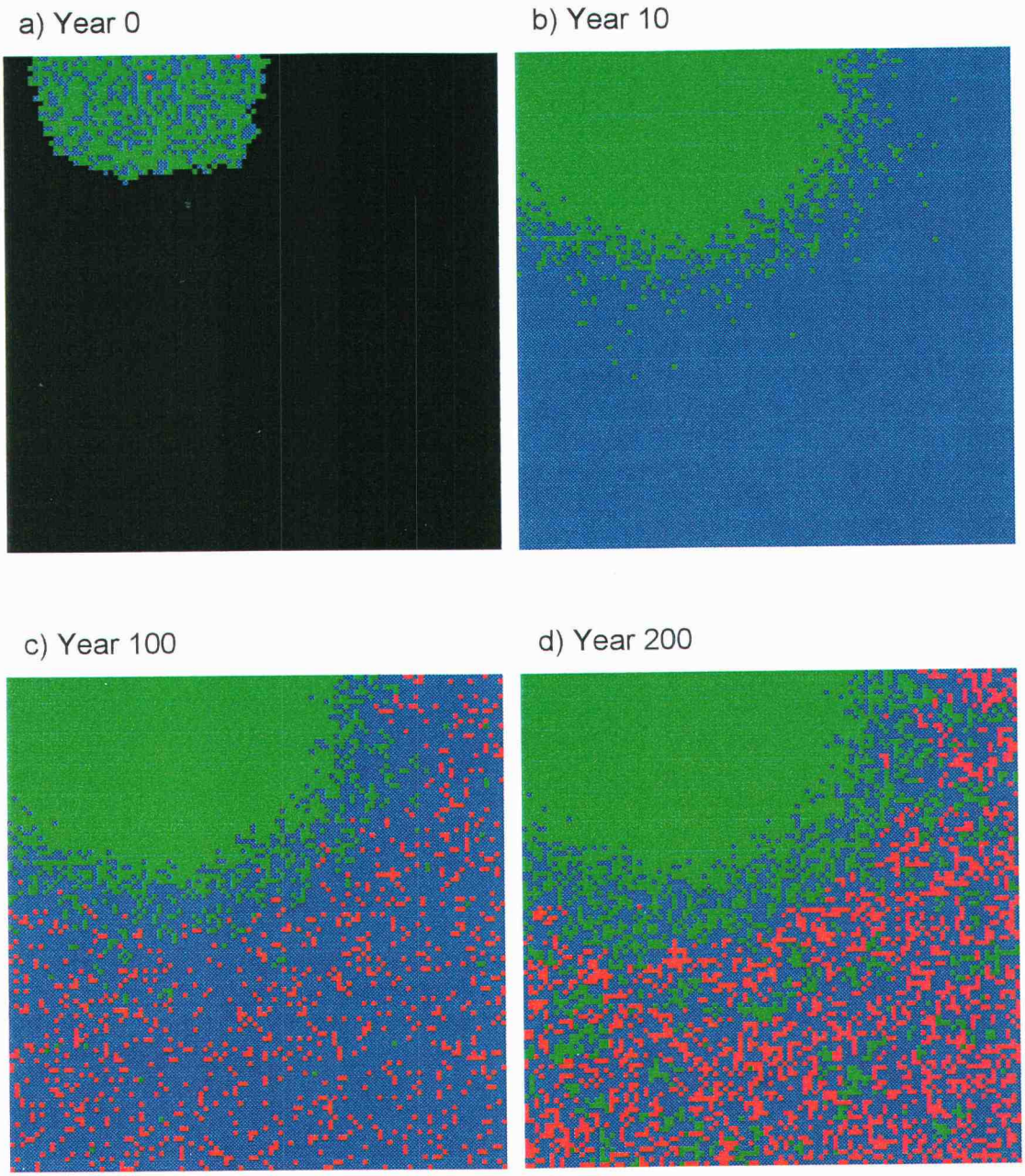
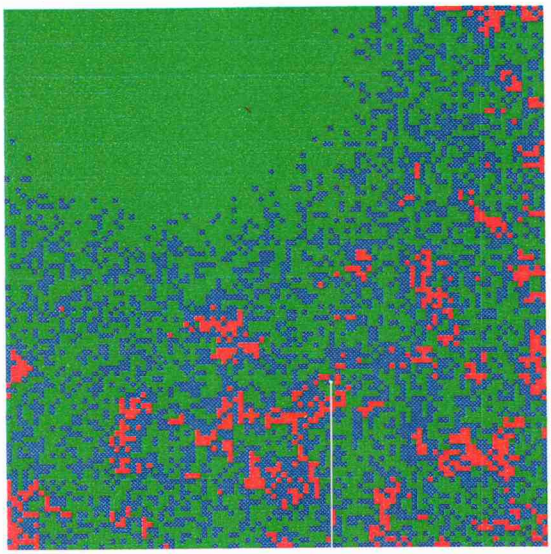


Figure 4.4: Results from a single model run with FRI=300, FSEV=0.9, PATCH=1, GRI=150, GREC=0.5, BDISP=0.0075. Cells are assumed to be 0.25 ha in size, and the 100 x 100 cell simulated landscape encompasses 6.25km². A fire occurs at year 0, leaving 10% of the landscape in a single remnant patch. Green cells represent mature and juvenile western hemlock, blue cells represent forest matrix without canopy gaps, and red cells represent forest matrix with canopy gaps.

e) Year 300



f) Year 400

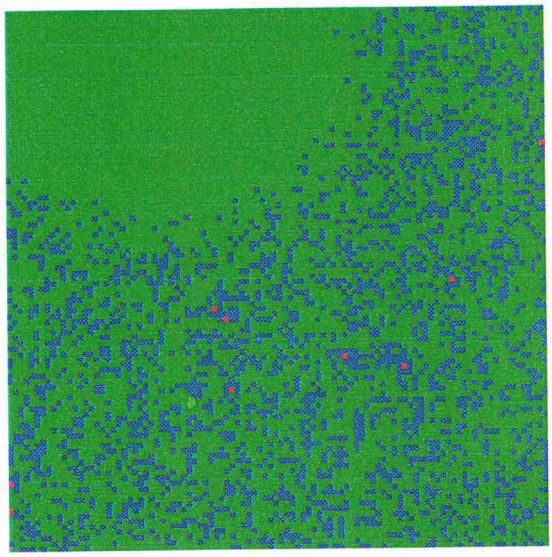


Figure 4.4 (continued)

even though some long-distance background dispersal events occurred and allowed new patches to establish far from the larger patch. Although these smaller patches had enlarged somewhat by 200 years after the fire, the overall distribution of *T. heterophylla* was still concentrated around the initial remnant patch.

When fire was heterogeneous and left more remnant patches, *T. heterophylla* establishment was distributed across a larger portion of the landscape than in the previous scenarios (Figure 4.5). The six initial patches rapidly coalesced into one large patch covering most of the landscape. When fire severity was very high, remnant patches were small and contained only a few mature *T. heterophylla* cells (Figure 4.6). In these cases, the post-fire range distribution of *T. heterophylla* was much smaller than in the lower-severity scenario. Although the patch sizes increased somewhat by year 200, *T. heterophylla* was still relatively uncommon in the areas furthest from the remnant patches.

T. heterophylla was particularly sensitive to variations in parameters describing the fire regime (Figure 4.7). *T. heterophylla* frequency increased with fire return interval (Figure 4.7a), but decreased with increasing fire severity (Figure 4.7b). *T. heterophylla* frequency also increased with remnant patch density, but this relationship was not as strong as with the other fire regime parameters (Figure 4.7c). The sigmoid response indicated that the increase was strongest between patch densities of three and seven, but relatively weak above and below this range. Parameters describing the gap dynamics regime had relatively weak relationships with *T. heterophylla*. *T. heterophylla* frequency decreased as the gap return interval increased from 100 to 300, but was not sensitive to increases above 325 (Figure 4.7d). *T. heterophylla* frequency also increased slightly with gap recruitment probability (Figure 4.7e) and background dispersal probability (Figure 4.7f).

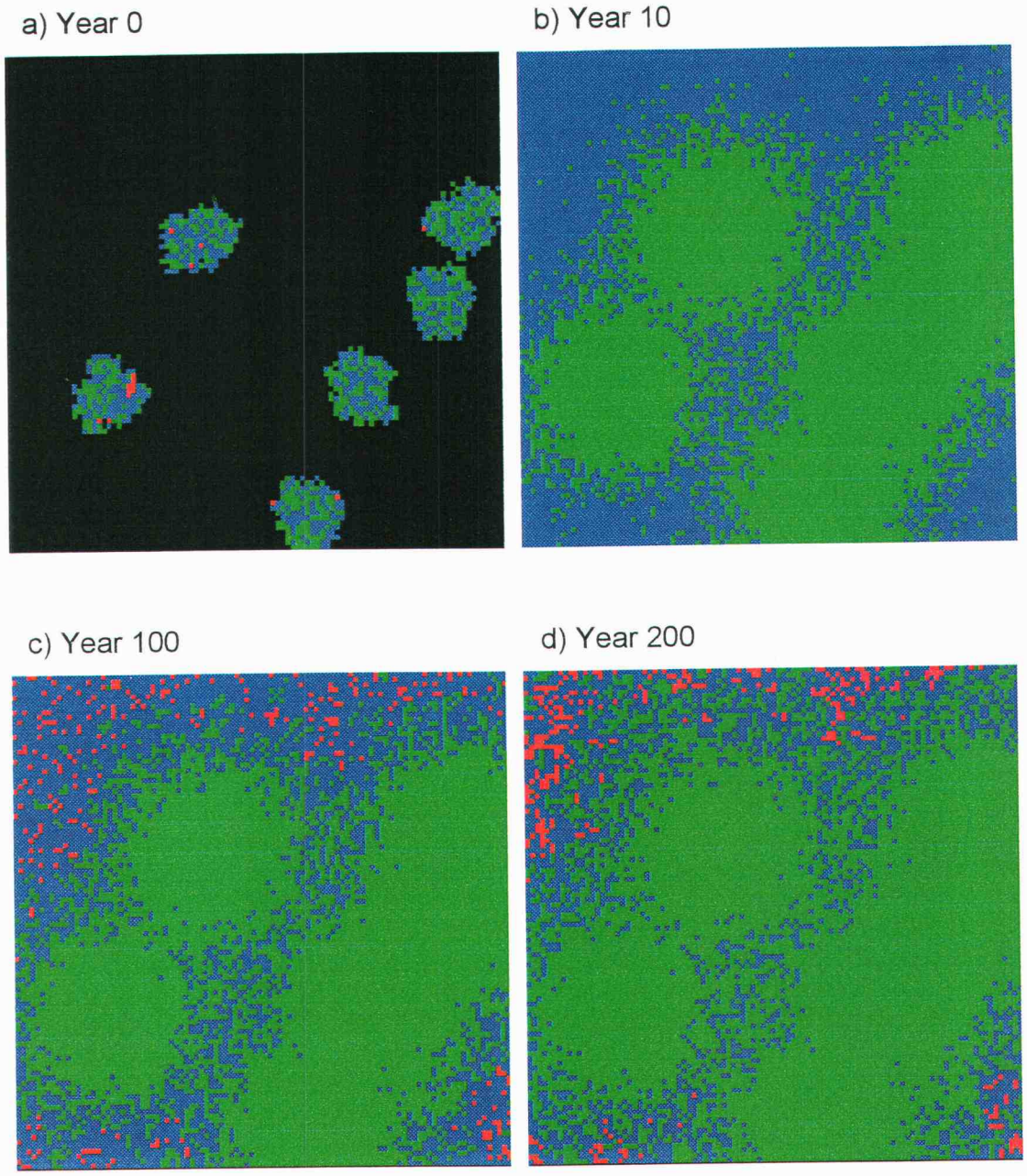


Figure 4.5: Results from a single model run with FRI=300, FSEV=0.9, PATCH=6, GRI=150, GREC=0.5, BDISP=0.0075. Cells are assumed to be 0.25 ha in size, and the 100 x 100 cell simulated landscape encompasses 6.25 km². A fire occurs at year 0, leaving 10% of the landscape in six remnant patches. Green cells represent mature and juvenile western hemlock, blue cells represent forest matrix without canopy gaps, and red cells represent forest matrix with canopy gaps.

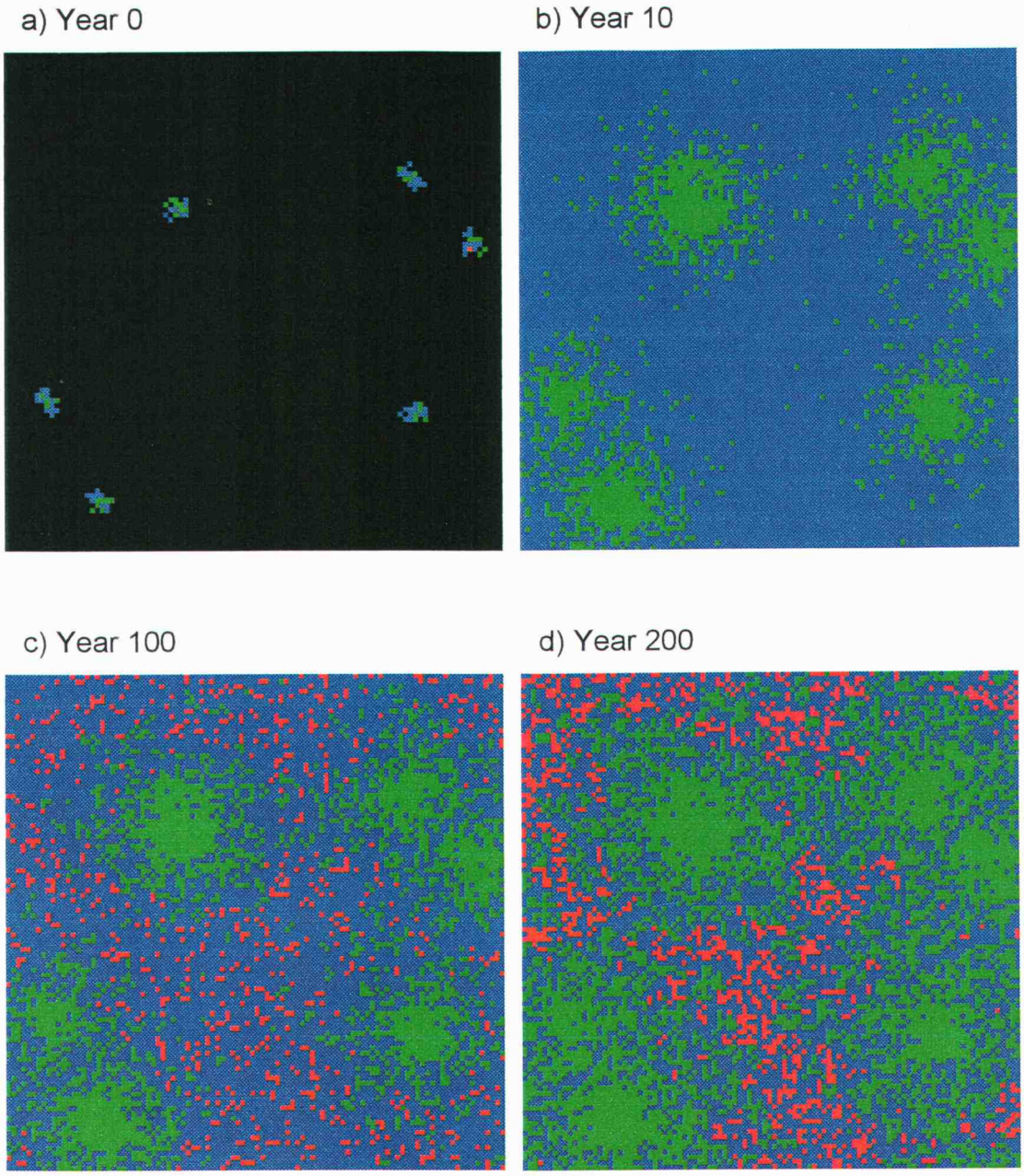


Figure 4.6: Results from a single model run with FRI=300, FSEV=0.99, PATCH=6, GRI=150, GREC=0.5, BDISP=0.0075. Cells are assumed to be 0.25 ha in size, and the 100 x 100 cell simulated landscape encompasses 6.25 km². A fire occurs at year 0, leaving 1% of the landscape in six remnant patches. Green cells represent mature and juvenile western hemlock, blue cells represent forest matrix without canopy gaps, and red cells represent forest matrix with canopy gaps.

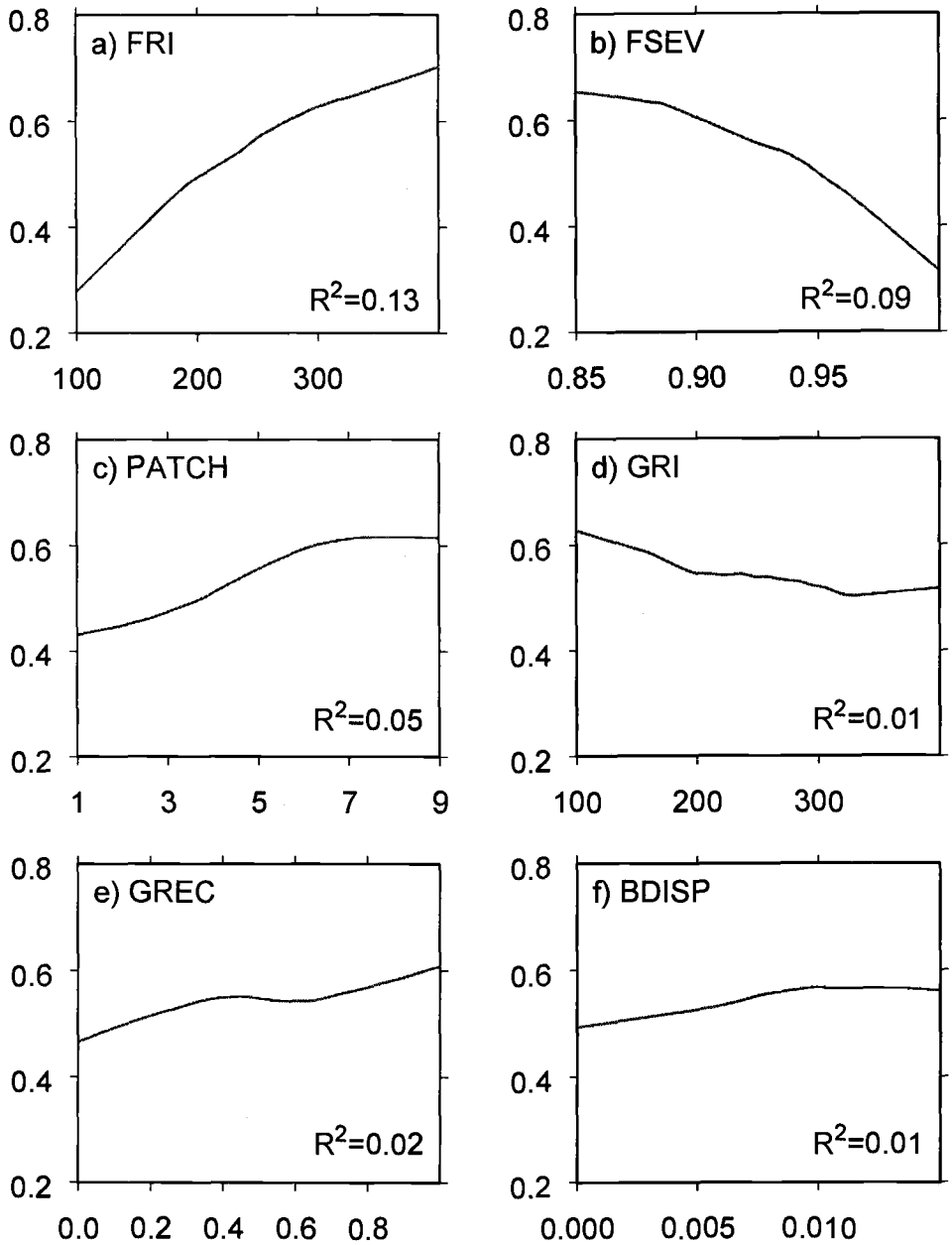


Figure 4.7: Locally weighted regression models predicting the proportion of cells on the landscape containing *T. heterophylla* as a function of a) fire return interval (years), b) fire severity (proportion of landscape burned), c) number of remnant patches, d) gap return interval (years), e) probability of establishment in canopy gaps and f) probability of background dispersal independent of seed source locations.

In addition to having a strong influence on *T. heterophylla* frequency, fire severity also had an interactive effect on several of the other parameters. Response to both gap recruitment probability and gap return interval was negligible at the highest severity values, but increased with decreasing fire severity (Figures 4.8). Remnant patch density also had a weak relationship with *T. heterophylla* at high fire severity, but had a much stronger relationship at low fire severity (Figure 4.9a). Fire severity had the opposite effect on the response to natural fire rotation – response was weakest at low fire severity, and strongest at high fire severity (Figure 4.9b).

When the fire return interval was decreased to 50 for a period of 50 years, *T. heterophylla* landscape frequency dropped to approximately 0.17 below the control level (Figure 4.10a). *T. heterophylla* frequency eventually returned to the control levels, although the 95% percent confidence interval did not consistently overlap zero until simulation year 600, 350 years after the high fire frequency period had ended. The landscape frequency of *T. heterophylla* showed much smaller drops when the fire return interval was decreased to 100 and 150 years (Figure 4.10b-c). Differences between the control and treatment were negligible when the fire return interval was only decreased to 200 years (Figure 4.10d).

Discussion

Results from the sensitivity analyses confirmed our intuitive expectations about *T. heterophylla* response to the various dispersal and disturbance parameters. Lower fire frequencies at the longer return intervals reflected more time between fires for the population to increase through gap-phase recruitment. Longer fire return intervals also decreased the probability that the landscape would burn and then reburn again within 30 years, before the trees established after the first fire had time to become reproductively mature. This "double-

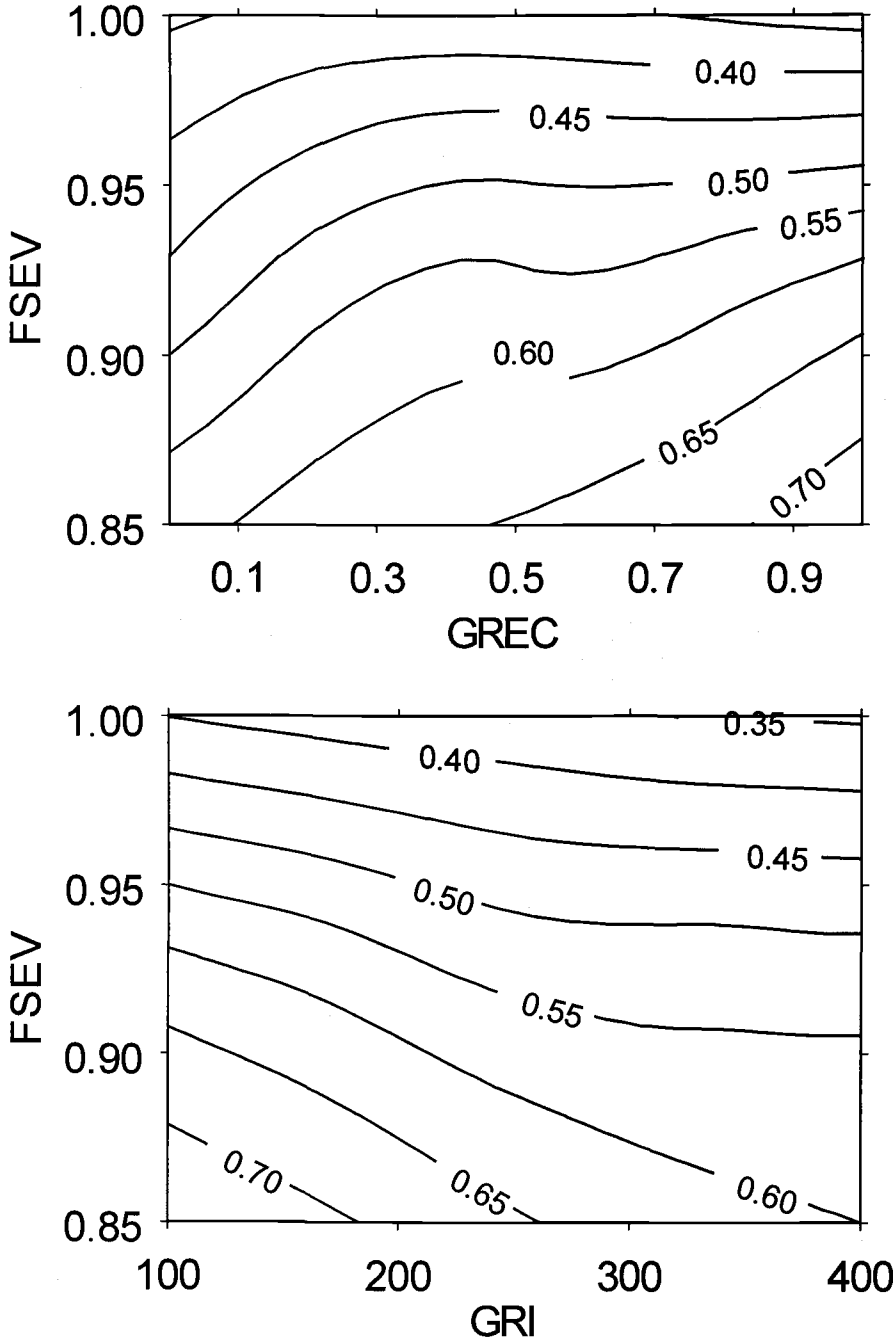


Figure 4.8: Contour plots of locally weighted regression models predicting The proportion of cells on the landscape containing *T. heterophylla* as a function of a) fire severity (FSEV) and remnant gap recruitment probability (GREC), and b) fire severity (FSEV) and gap return interval (GRI).

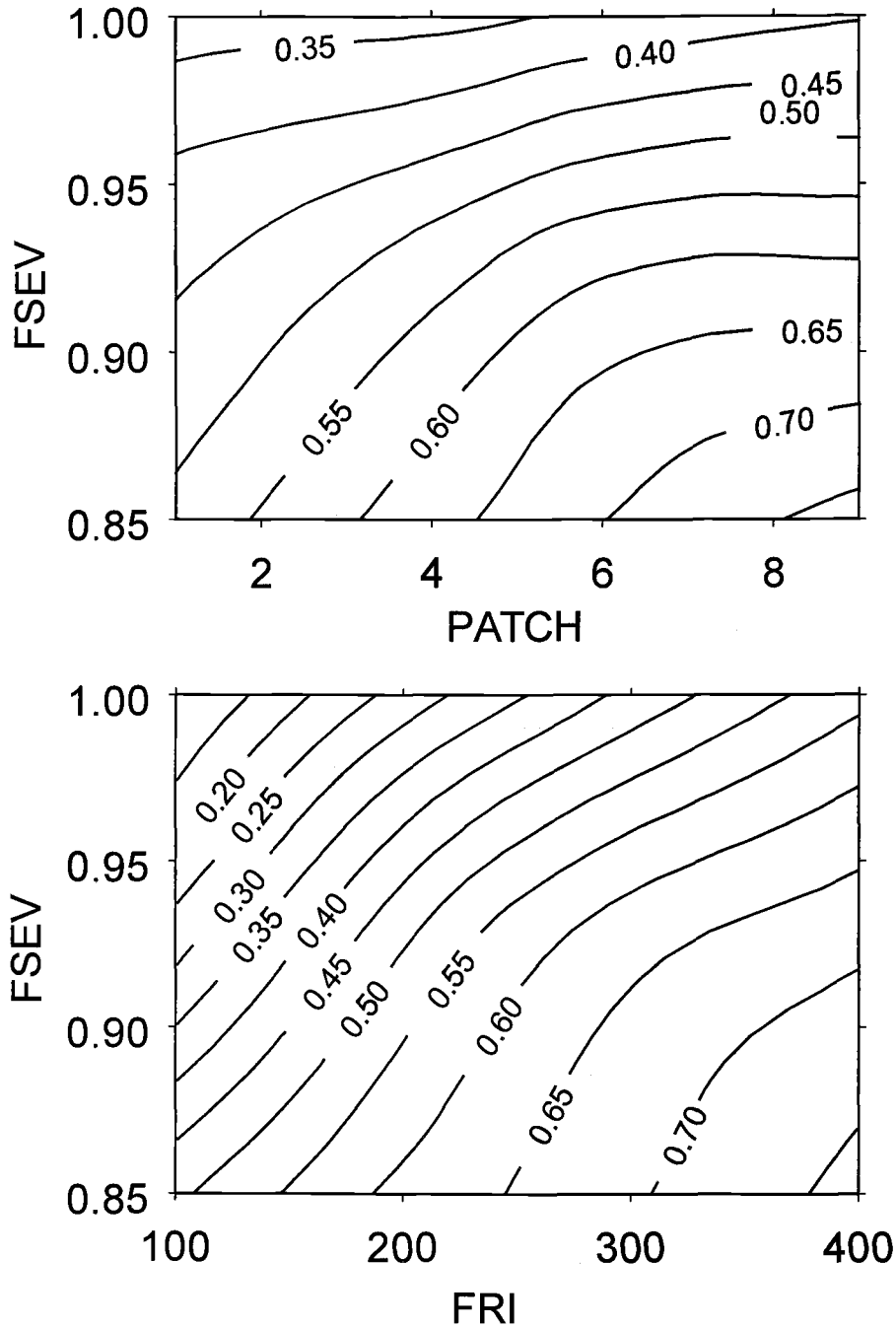


Figure 4.9: Contour plots of locally weighted regression models predicting the proportion of cells on the landscape containing *T. heterophylla* as a function of a) fire severity (FSEV) and remnant patch density (PATCH), and b) fire severity (FSEV) and fire return interval (FRI).

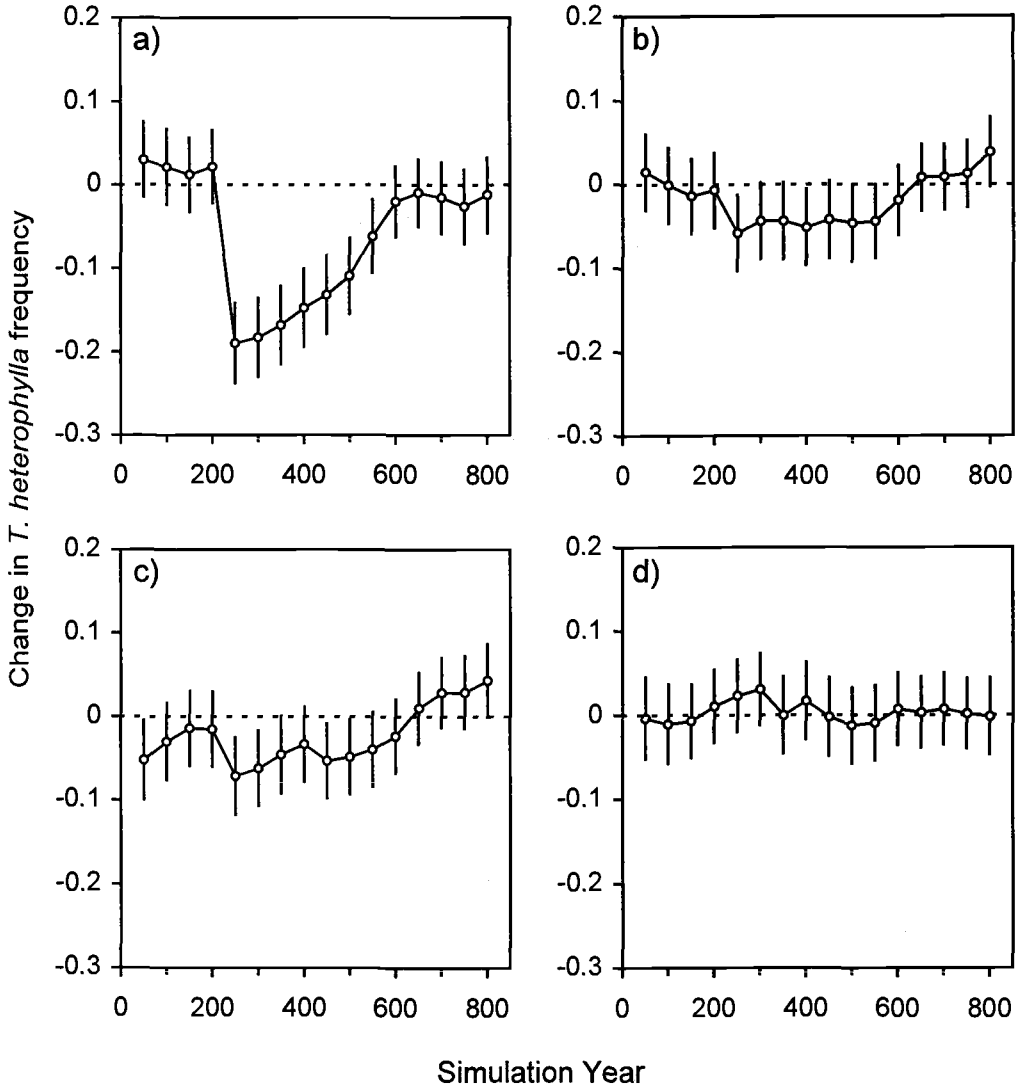


Figure 4.10: Differences in the proportion of cells containing *T. heterophylla* on the landscape between the mean of 100 treatment runs and the mean of 100 control runs computed at 50-year intervals for four different time series of fire frequencies. The control run was made at a fire frequency of 300 for the entire 800 years. The treatment scenarios began at a mean fire return interval of 300 for years 0-200. The mean fire return interval decreased between years 200-250 to a) 50, b) 100, c) 150, and d) 200, and was then returned to 300 for years 250-800. Error bars represent 95% confidence intervals for the differences between the mean values. Other parameter values are listed in Table 4.1.

burning" effect has been shown to have a strong influence on populations of other fire-sensitive, dispersal-limited species (Bradstock et al. 1996). In contrast, longer gap return intervals reduced *T. heterophylla* frequency by limiting the number of cells on the landscape where overstory recruitment could occur in canopy gaps (Figure 4.3). Low fire severity increased *T. heterophylla* frequency because remnant patches were larger and contained more *T. heterophylla* cells than when fire severity was low (Figures 4.5-4.6). High remnant patch densities tended to distribute seed sources across more of the landscape than low remnant patch densities, which made it more likely that a given cell would have one or more reproductively mature neighbors to facilitate recruitment in canopy gaps. Background dispersal increased recruitment both after fires and in canopy gaps, and provided an opportunity for new dispersal foci to establish at sites remote from existing seed sources.

The fire return interval and fire severity parameters explained more of the variation in *T. heterophylla* frequency than any of the other parameters we tested. The generally weak response to gap recruitment was particularly surprising, because we considered a range of values from zero (recruitment in gaps almost never occurs) to one (recruitment in gaps occurs immediately if a neighboring seed source is present). Rates of populations increase through gap-phase recruitment are limited by the requirement that a canopy gap be adjacent to a seed source before dispersal can occur and by the time lag required for newly recruited *T. heterophylla* to reach reproductive maturity. These constraints probably also limit the influence of isolated, background dispersal events on rates of populations expansion.

These results suggest that when understory dispersal distances are very short, factors that affect the probability of gap recruitment such as resource levels, substrate availability and competition from other plants may have relatively little influence on species distribution at the landscape scale. Although fine-scale habitat features may exert a strong influence on the

amount of regeneration within a particular gap where seed sources are present, the frequency and pattern of pattern of large-scale fires may ultimately control the abundance of *T. heterophylla* at the landscape scale through dispersal limitations. High sensitivities to fire-related parameters reflect the fact that fires have the potential to rapidly alter *T. heterophylla* pattern and abundance, because fire-induced mortality and post-fire reestablishment both take place within a single time-step of the model.

The interactions among fire severity, fire frequency and remnant patch density demonstrate the complex effects that various components of a fire regime can have on populations of a disturbance-sensitive species. Fire severity controls the total area of remnant patches, while remnant patch density affects the spatial distribution of these patches across the landscape. When severity is high, the total areas of remnant patches is very low and the potential for seed dispersal from these patches is so limited that their pattern has little effect on *T. heterophylla* population growth. As fire severity decreases, however, a larger amount of post-fire seed sources becomes available and distributing these sources across a larger area of the landscape has the potential to significantly increase the size of the post-fire *T. heterophylla* cohort. Low fire severity also decreases sensitivity to the fire return by interval reducing the amount of post-fire mortality and increasing the amount of post-fire recruitment relative to high severity fires.

The interactions among fire severity, gap return interval, and gap recruitment probability illustrate how an ecological response to a process operating at a particular scale can be constrained by processes operating at larger scales. When fires were severe, *T. heterophylla* exhibited a negligible response to changes in gap return interval and gap recruitment probability. In the high-severity scenarios, few remnant *T. heterophylla* were present to disperse seeds following fires, and subsequent population increases were limited by

the low number of seed sources on the landscape (Figure 4.6). Increases in gap creation or recruitment had little effect on rates of population increase where seed sources were not present. When fire severity was low, *T. heterophylla* was distributed across broader areas of the landscape and more pixels had an adjacent seed source. In these cases, increased rates of gap formation and recruitment had the potential to increase the rate of population growth (Figure 4.5.).

The results of the experimental simulations supported our hypothesis that periods of high fire frequency can lead to sustained decreases in the landscape frequency of *T. heterophylla.* The effect of decreasing the fire return interval from 300 years to 50 years was pronounced, whereas the effects of decreasing the fire return interval to 100, 150, or 200 years was negligible (Figure 4.10). These results are indicative of a threshold response to changes in fire frequency, and suggest that *T. heterophylla* populations may be affected dramatically if fire frequency suddenly drops below a certain value. In contrast, *T. heterophylla* population fluctuations may be buffered against smaller temporal variations in fire frequency.

Because these results were derived from a relatively simple, non-validated model, they cannot be interpreted as conclusive evidence that historical increases in fire frequency are responsible for the low amounts of *T. heterophylla* in many areas of the Coast Range. The results do, however, corroborate observational data that supports this hypothesis. As mentioned in the introduction, several studies have found that the amount of overstory *T. heterophylla* is lower in areas that burned and then reburned once or more within a short time period, suggesting that increased mortality from the multiple burns led to seed source limitations that limited the amount of post-fire establishment on these sites. These patterns have been found in areas ranging from the Oregon Coast Range (Poage 1995), to the central

Oregon Cascades (Klopsch 1985), to the southern Washington Cascades (Gray and Franklin 1997).

In the Cummins Creek Wilderness, which burned several times between 1850 and 1910, *T. heterophylla* basal area decreased with distance from remnant old-growth patches (Chapter 2). This pattern was interpreted as evidence that decreases in seed dispersal with distance from the remnant patches influenced the spatial pattern of *T. heterophylla* establishing after the fires. Current frequency of *T. heterophylla* advance regeneration also decreases with distance from the old-growth remnants, suggesting that the legacy of the historical fires influences ecological response to canopy gaps through seed sources limitations in the current overstory (Chapter 3). Taken as a whole, this empirical evidence suggests that both the temporal and spatial patterns of fires affect the post-fire patterns of *T. heterophylla*, and that this pattern constrains the operation of subsequent gap dynamics on the landscape through seed source limitation. Our simulations lend support to this hypothesis by showing that it is reasonable to expect a sustained drop in the amount of *T. heterophylla* in a landscape following a brief period of intensive disturbance given our current assumptions about *T. heterophylla* life history, dispersal, and response to disturbance.

As with any model-based research, the results of this study must be interpreted in light of the simplifying assumptions that were made in developing the model. If there are real-world situations where this particular set of assumptions do not hold, then we would expect systems to behave differently than predicted by the model. We assumed, for example, that the probability of gap disturbance in a given cell was the same during all time periods, and was independent of gap disturbances in other cells. In addition, we assumed that dispersal into closed canopy forests was always 50 m or less, with the exception of rare, background dispersal events. One type of scenario where these assumptions might be invalidated is a large

windstorm that blows down many patches of trees scattered across the landscape. The same windstorm might also precipitate numerous long-distance dispersal events, creating a pulse of overstory recruitment across large areas and rapidly expanding the distribution of *T. heterophylla*.

Other ecological processes not included in the current model could also influence the rate of *T. heterophylla* dispersal. In the Oregon Coast Range, aggressive clonal shrubs such as *Rubus spectabilis* can invade gaps and form dense, low canopies (Tappeiner et al. 1991). If *T. heterophylla* advance regeneration is not present before gap formation, or if mature trees are not present nearby to facilitate rapid establishment of seedlings, the probability of successful establishment in the gap might be greatly reduced once the shrub layer is established. Spatial variability in the environment was not considered in our model, and might also impact the spatial dynamics of *T. heterophylla*. Shrubs such as *R. spectabilis*, for example, grow most rapidly on moist sites such as riparian areas and lower hillslopes. If shrub competition reduces *T. heterophylla* establishment in these patches, they could serve as barriers to gap-phase dispersal through closed canopy forests. The distribution of *T. heterophylla*, as with other species, may also tend to be patchier near the borders of its range where climatic conditions are less favorable and suitable habitats are restricted (Jeffries et al. 1983).

Although our model was focused on the population dynamics of *T. heterophylla*, we might expect other late-successional plant species with comparable life-history characteristics to behave in a similar manner. *Abies amabilis* (Pacific silver-fir), for example, is a late-successional, fire-sensitive species lacking a persistent seed bank that establishes in canopy gaps at in high-elevation forests (Stewart 1986). As with *T. heterophylla*, we would hypothesize that the distribution of *A. amabilis* at the landscape scale is sensitive to the frequency and pattern of fires. The aboveground portions of most understory plants are also

fire-sensitive, but many of these species have the ability to persist in the soil bank following disturbance as dormant seeds, rhizomes or tubers (Erikson 1996). We can envision that the spatial population dynamics of these species might be somewhat similar to that of *T. heterophylla*, but would operate at a much smaller scale. Following a fire, understory plants might initially emerge in a few, isolated remnant pockets, and their populations would slowly diffuse into the rest of the stand over a period of decades or centuries.

Our model considered fire as the primary coarse-scale disturbance factor, but it is also possible that anthropogenic disturbances such as timber harvesting might have similar effects on the pattern and dynamics of some tree species. In the Great Lakes region, for example, large-scale logging followed by selective cultivation of high-value tree species has been invoked as one of the factors limiting seed sources of *Tsuga canadensis* (eastern hemlock) over much of this region (Mladenoff and Stearns 1993). In the Pacific Northwest, *P. menziesii* is selectively planted in many managed forest stands. While naturally regenerating *T. heterophylla* are seldom completely excluded from these plantations, low overstory densities could reduce seed availability and limit the development of multilayered forest structure as these stands age. Low levels of *T. heterophylla* and other shade-tolerant species could be particularly problematic in planted stands located in old-growth reserves on federal land, where the current management focus is on encouraging rapid development of late-successional structure.

Conclusions

We consider our model to embody a general working hypothesis of *T. heterophylla* landscape dynamics. Our simulations suggest that wildfires have the potential to rapidly change the abundance and pattern of *T. heterophylla* populations within a landscape. Gap

dynamics, in comparison, alter the spatial distribution of *T. heterophylla* relatively slowly. In our simulations, the movement rates through closed canopy forests was limited because understory regeneration only occurred within a short distance of parent trees, and because one or more canopy gaps was required for understory regeneration in a given cell to reach the overstory. Even when a gap did occur adjacent to a seed source, there was still a lag period before the newly recruited individuals reached reproductive maturity and could continue the dispersal process. In situations where this basic set of assumptions holds, we hypothesize that stands with little or no overstory *T. heterophylla* present may not develop the multilayered canopies characteristic of old-growth forests within the time frames of current management plans. Instead, it may possibly take centuries for trees to diffuse into these areas from adjacent patches or nucleate outward from isolated refugia. We recommend that researchers explicitly consider the influences of both disturbance and dispersal when studying current patterns of *T. heterophylla* and similar fire-sensitive, late-successional species, and when developing methodologies to project current landscape patterns into the future.

CHAPTER 5: Conclusions

Overview

No single ecological mechanism was sufficient to explain all of the variability in forest vegetation at the watershed scale. To some extent, the particular factor that best explained the observed patterns depended on the manner in which vegetation was described. For example, hillslope community composition was primarily related to environmental variables (Chapter 2). This result supports a gradient-based view of forest communities in which the species found at a given site depends mainly on the local physical environment (Hutchinson 1957, Whittaker 1967). This concept of relatively stable, predictable community patterns forms the basis for the use of plant community composition to classify habitat types (Daubenmire 1976, Cook 1996). My results suggest that it is possible to make meaningful inferences about the environmental characteristics of a given site based on forest community composition, although historical factors may confound interpretations based on dispersal-limited species such as *Tsuga heterophylla* (western hemlock). The strongest environmental gradient in the study area encompassed change from *Picea sitchensis* (Sitka spruce) dominated sites in coastal areas to *Pseudotsuga menziesii* (Douglas-fir) dominated sites further inland (Chapter 2). Based on this relationship, I was able to use physiographic variables derived from digital elevation models and stream maps to predict more than half of the spatial variability in *P. sitchensis* advance regeneration (Chapter 3).

In contrast to the compositional patterns, hillslope forest structure was primarily related to recent fire history. Young stands with no old-growth remnants had small trees, little dead wood, and a simple single-layered structure. Old stands and stands with remnant old-growth trees had larger tree sizes, accumulations of dead wood in the form of snags and down

logs and complex, multilayered structure. Relatively little of the variation in forest structure was correlated with the physical environment or physically structured disturbance variables. These relationships suggest a variable landscape mosaic in which disturbance controls the pattern of forest structures across the landscape, but the type of structure found in a particular place at a given time is not predictable based on physical landscape characteristics (Borman and Likens 1979, Oliver 1981, Turner et al. 1993). In my vegetation mapping exercise, however, I was able to predict some of the variability in stand structure variables such as overstory crown size and conifer/hardwood composition using remote sensing-based measurements of the forest canopy (Chapter 3). *T. heterophylla* regeneration was most likely to be found under large conifer canopies, suggesting that the potential for understory regeneration may increase over time as successional and structural development progresses.

In addition to site-level predictor variables related to the physical environment and stand age structure, landscape-scale patterns of disturbance history played a role in structuring forest patterns. The basal area of *T. heterophylla* and *P. sitchensis*, for example, decreased with distance from old-growth patches (Chapter 2). I hypothesized that these patterns arose as a result of seed dispersal gradients following historical fires (Chapters 2,3). Dispersal pattern at the time of stand initiation is an example of the type of historical factor that is generally not measured when studying vegetation patterns, and typically becomes part of the random error associated with these analyses (McCune and Allen 1985). I was able to incorporate historical seed source limitations into the predictive models of *T. heterophylla* understory regeneration using maps of existing old-growth patches derived from aerial photographs. Because of short dispersal distances in closed-canopy forests (Schrader 1998) *T. heterophylla* advance regeneration is tightly linked to overstory patterns and declines with distance from old-growth patches.

Dynamic simulations of *T. heterophylla* populations demonstrated that fine scale processes related to the rates of gap formation and seedling recruitment in canopy gaps may have only minor influences on the distribution of *T. heteorphylla* at the landscape scale (Chapter 4). Instead, the frequency and severity of fires and other large disturbance that kill *T. heterophylla* may have the strongest impact. Although fine-scale habitat features are known to influence regeneration in gaps when seed sources are present, the frequency and pattern of pattern of large-scale fires may ultimately control the abundance of *T. heterophylla* at the landscape scale by killing large patches of trees and setting up dispersal-limited recruitment gradients. The simulations also indicated that brief increases in fire frequency could lead to dramatic and sustained decreases in the amount of *T. heterophylla* on the landscape once fire frequency is reduced below a threshold value. These results suggest a multiple pathway model in which succession at a particular site may vary depending on disturbance history and its influence on the initial mix of species at a site (Egler 1954, Noble and Slatyer 1980). For example, forests that establish near a *T. heterophylla* seed source may rapidly succeed to multilayered forest as understory *T. heterophylla* grow into gaps in the forest canopy. Stands that establish without a nearby *T. heterophylla* seed source may instead develop *T. heterophylla* dominance and multilayered canopies very slowly because few *T. heterophylla* are present to recruit into the overstory.

The influences of floods, debris flows, and other disturbances on riparian vegetation have been well-documented (Hack and Goodlett 1960, Hupp 1982, Swanson et al. 1998). My study, however, found that disturbance variables accounted for only minor portions of the expalined variability of stand structure and community composition in riparian areas. I did find strong correlations between vegetation characteristics and measurements of the channel network. At the watershed scale, measurements of stream order, stream gradient, and valley

floor width may integrate finer scale patterns and processes related to the distribution of valley floor landforms, the energy of moving water and sediment, and the influences of channel constraint. Although my results did not provide details on the specific processes related to riparian vegetation patterns, they do suggest that watershed-scale variables can provide a framework for predicting landscape scale riparian vegetation patterns. Indicator variables for riparian areas, for example, were used in the predictive models of both *P. sitchensis* and *T. heterophylla* advance regeneration (Chapter 3).

Because my research was based on a relatively small landscape studied at a single point in time, I hesitate to use it to derive specific recommendations for management and conservation efforts in other areas. Perhaps the most important general lesson is that watershed-scale vegetation patterns are structured by a complex array of ecological processes. Some of this complexity can be resolved by recognizing that different forest vegetation attributes (composition vs. structure) may be related to different sets of controlling variables (environment vs. disturbance). In addition to local environment and disturbance history, vegetation at a particular site is also influenced by dispersal limitations linked to landscape-scale biotic patterns that are the legacy of past fires. Complexity can be reduced in some cases by choosing an appropriate scale for analysis. For example, although fine-scale details of riparian disturbance are difficult to measure and relate to vegetation patterns, watershed-scale indices based on position in the channel network may effectively integrate much of the variability in riparian environments and disturbance regimes. Efforts to develop watershed management plans based on a coarse-filter conservation strategy will need to consider the full range of processes operating at the watershed scale and their influences on the pattern and abundance of different forest types. Strategies that are narrowly based on simplistic ecological

frameworks or single ecological processes may fail to account for the full range of variability in forest vegetation patterns.

Conclusions

1. A large fire burned most of the Cummins Creek Wilderness in the mid-19th century. Old growth is uncommon and concentrated in a few remnant patches. Old-growth patches were not associated with riparian areas or other moist sites.
2. Subsequent reburns on many sites have created a resulted in landscape mosaic of stands currently 80-120 years in age. Reburns appear to have been more frequent on the dry upper hillslopes than on lower hillslopes and in riparian areas.
3. Floods and debris flows in riparian areas have led to the establishment of relatively young (20-40 year old) alder cohorts along many streams. Other disturbance agents such as wind, disease, and insects have had a comparatively minor influence on forest structure and composition within the study area.
4. On hillslopes, community composition gradients were mostly related to environmental variables, while forest structure gradients were primarily correlated with disturbance variables.
5. Basal area of both *T. heterophylla* and *P. sitchensis* decreased with distance from remnant old-growth patches. I hypothesized that the old-growth patches served as disturbance refugia for these fire-sensitive species, and that current patterns reflect post-fire dispersal gradients.
6. In riparian areas, disturbance variables had relatively weak relationships with forest composition and structure. I believe this result reflects the difficulty in adequately quantifying complex riparian disturbance regimes rather than suggesting that disturbance is unimportant in riparian areas. Both composition and structure were correlated with

physiographic variables describing the drainage network, and these variables may integrate unmeasured elements of riparian disturbance regimes.

7. Coastal riparian areas (< 5 km from the ocean) had exceptionally high densities of conifer regeneration compared to other portions of the study area. *P. sitchensis* comprised the majority of seedlings and saplings in coastal riparian areas. Possible reasons for these high regeneration densities include low moisture stress during the growing season because of coastal fog, high volumes of down wood to serve as regeneration substrates, high levels of browsing that may reduce shrub competition, and high light levels under the open riparian forest canopy.
8. Although I found statistically significant relationships between understory conifer patterns and GIS predictor variables, the models explained only low to moderate amounts of the overall variability.
9. Maps produced using fixed cutoff values to predict presence/absence and a mean response to predict abundance produced a deceptive picture of the level of precision in the mapping. When models only explain low to moderate portions of the observed variation, predictive maps are better interpreted as qualitative trends rather than precise quantitative predictions.
10. Short seed dispersal distances in closed-canopy forests, the requirement for canopy gap disturbances to facilitate overstory recruitment, and the lag time between recruitment and reproductive maturity result in slow rates of *T. heterophylla* population spread through closed-canopy forests.
11. Although fine-scale habitat characteristics are known to influence regeneration within a gaps where seed sources are present, the frequency and pattern of pattern of large-scale fires may ultimately control the abundance of *T. heterophylla* at the landscape scale through recruitment limitations.

12. Brief increases in fire frequency can cause sustained decreases in the amount of *T. heterophylla* on the landscape and reduced rates of population recovery once fire frequency is reduced below a threshold value.

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APPENDIX

A History of Human Land Use in the Cummins Creek Area, Lane County, Oregon

Introduction

Human activities are often viewed as a confounding factor in ecological research, where many studies have focused on characterizing "natural" patterns and processes. It is difficult, however, to find any North American landscape that has not been influenced by humans to at least some degree. Humans lived on this continent for thousands of years before the first European settlers arrived, affecting the native ecosystems through hunting, burning, gathering, and agriculture. Euroamerican settlement has led to the permanent conversion of many ecosystems through development, agriculture, and resource extraction. Introduction of non-native species has also altered the structure of many native communities. As our technology has advanced in the 20th century, so has the rate and degree to which we can alter the natural world. Although we have chosen to preserve some lands as parks and wilderness areas, the selection of these reserves is often governed as much by historical and political factors as by ecological considerations.

As part of my doctoral dissertation, I undertook a study of watershed-scale vegetation patterns in the Cummins Creek Wilderness, located on the Oregon Coast. I also examined the social history of the area to gain a better understanding of how humans have altered the landscape, and of how the environment shaped the culture and lifestyle of humans in the area. This social history can be categorized into three broad periods: the period of habitation and use by native American tribes before 1850, the period of homesteading by Euro-American settlers from approximately 1880 until 1930, and a modern period that encompassed limited timber extraction followed by an emphasis on preservation and scientific research.

The Native Inhabitants

The aboriginal inhabitants of the Cummins Creek area belonged to the Alsea tribe. The dividing line between Alsea and Siuslaw territories was located at the mouth of Tenmile Creek, just to the south the Cummins Creek Wilderness (Figure 1, Siuslaw National Forest 1995). Archaeological sites near the mouths of Cummins and Bob Creeks contain remnants of middens—large piles of shells and other discarded debris (Figure 2, Minor 1986). Several of these sites also appear to have vestiges of housepits. These shallow depressions formed the foundations of the dwellings of the Alsea and other coastal tribes. They were covered by pole-framed, cedar-shingled structures to provide shelter (Buan and Lewis 1991). The exact nature of these sites is not entirely clear. One source suggests that they were temporary camps used during seasonal trips up and down the coast for fishing trading, and hunting (Siuslaw National Forest 1995). Another source, however, interprets the large sizes of many of the middens along with the presence of housepits as evidence of long-term dwellings at the mouths of Cummins and Bob Creeks (Minor 1986).

Like other coastal tribes, the Alsea were a society of hunter-gatherers, who gleaned most of their sustenance from the ocean (Buan and Lewis 1991). Coho salmon was fished from rivers and estuaries during the early fall runs, and steelhead were harvested in the winter months. Ocean fish such as smelt, herring, flounder, and perch were also harvested throughout the year. Other seafood such as clams, mussels and crabs were collected from estuaries, tide pools, and bays. In comparison to the coast and rivers, the inland forests were not a major food source for the Alsea, although deer, elk, beaver, and quail were occasionally hunted (Aikens 1982). Forest plants such as salmonberry, skunk cabbage, huckleberries and blackberries were important food sources. The forests also provided wood and other materials for making dwellings, clothing, baskets, weapons and other tools. There is little evidence to

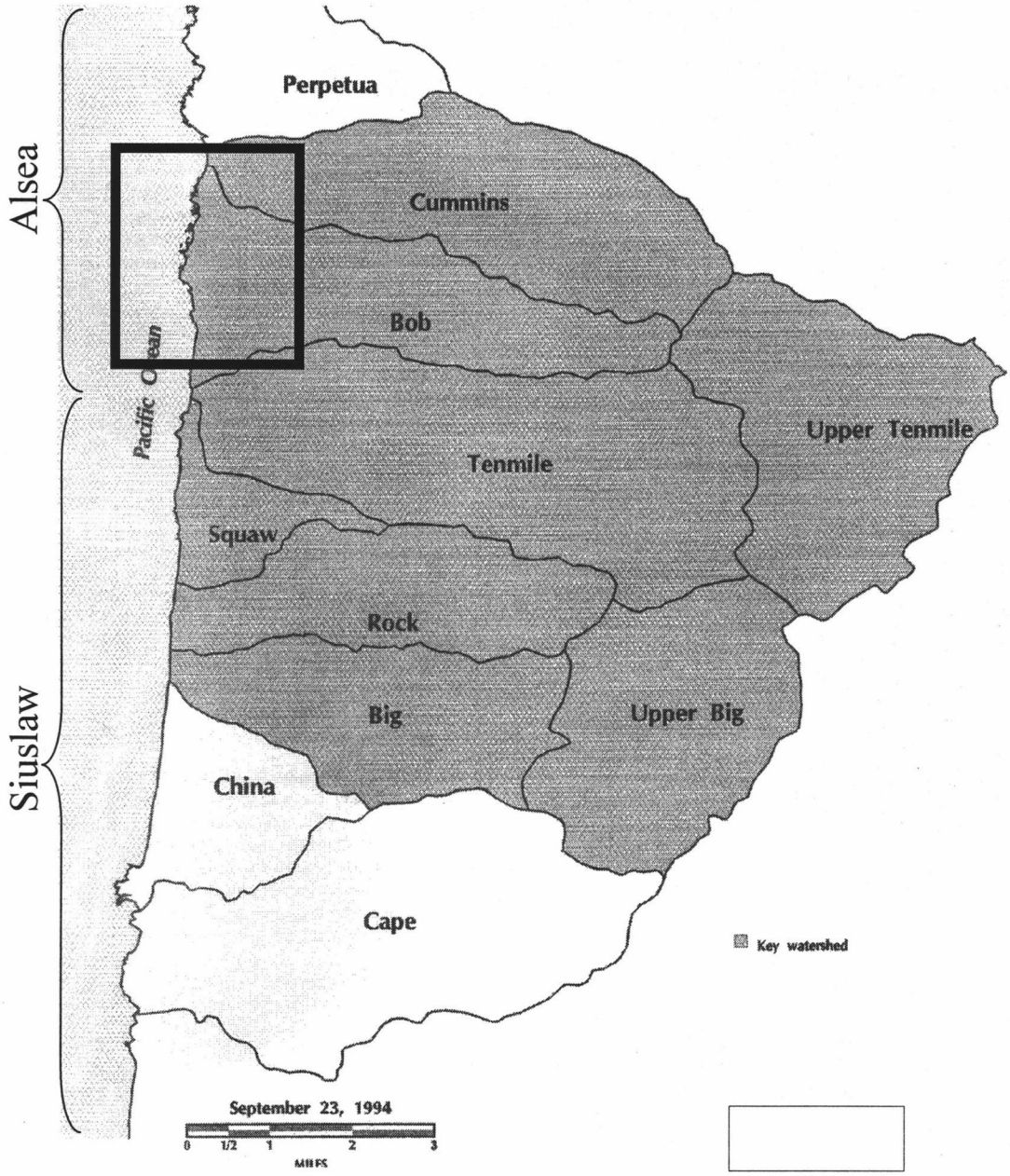

Figure 1: Map of subwatersheds in the Cummins Creek area, with terrirories of the Alsea and Siuslaw tribes outlined. The dark rectangle delineates the area detailed in Figure 2.

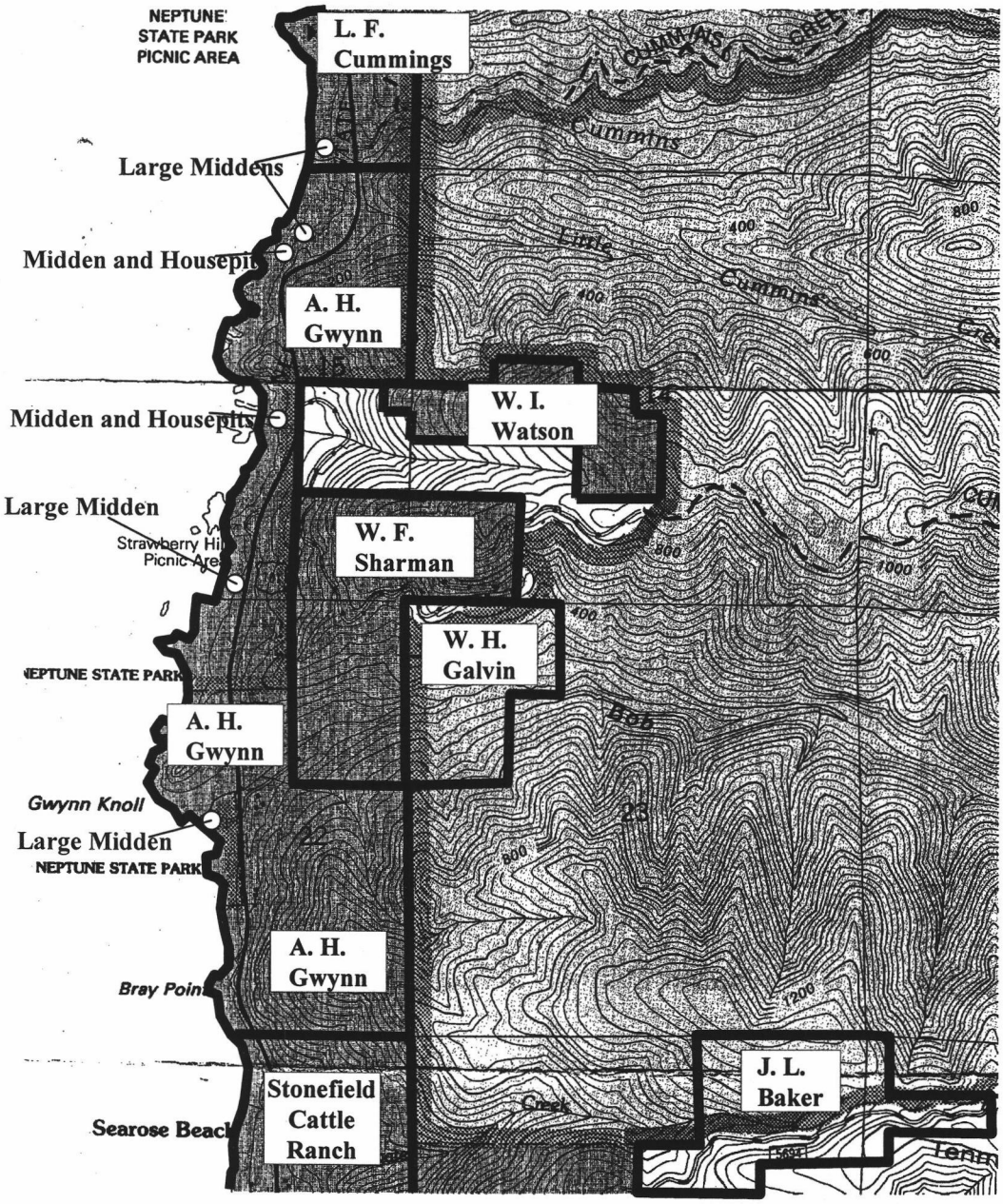

Figure 2: Map of historical settlements near the Cummins Creek Wilderness Area. White circles denote archeological sites with evidence of habitation by the native Alsea. Bold black lines delineate land homesteaded under the Homestead Act of 1862 and the Forest Homestead Act of 1907.

suggest that the Alsea made extensive use of fire for vegetation management as did the Kalapooyia and other Willamette Valley tribes, although one source suggests that it may have been used to maintain some ridgetop trails and coastal meadows (Siuslaw National Forest 1995).

Aside from the shreds of information that can be gathered from archaeological records, little specific information about aboriginal use of the Cummins Creek area is available. Interviews by the anthropologist John Harrington, however, provide some additional tantalizing details. Harrington was particularly interested in ethnogeography - identifying place names and their meanings (Buan and Lewis 1991). In 1942 Harrington conducted a boat trip along the coast with several informants, including Frank Drew, a member of the Coos tribe who had lived at the Alsea sub-agency in Yachats until 1875. Drew identified a point near the mouth of Cummins Creek as a spot where hunting parties would leave the coast to travel inland. Drew also indicated that the aboriginal name for Bob Creek meant "Place of the Dead Alsea" or "Place where they buried the Alsea". It is not clear from the notes whether this name referred to a particular individual who had died near Bob Creek, or more generally indicated a burial area in the vicinity. A prehistoric burial was excavated from a site near the mouth of Bob Creek (Minor 1986), but there is not sufficient evidence to conclude whether or not this area was actually a burial ground.

When Euro-American settlement began in the mid-nineteenth century, the Cummins Creek area was originally designated as part of the Coast Range Reservation (later known as the Siletz Reservation), a 1,382,400 acre tract that ranged from Cape Lookout in the north to the Siltcoos River in the South (Hays 1976, Siuslaw National Forest 1995). All of the native peoples in western Oregon were relocated to this reservation. After 1860, members of the Coos and lower Umpqua tribes were forced onto this reservation and settled at the Yachats

sub-agency, located near the mouth of the Yachats River just five miles to the north of Cummins Creek (Siuslaw National Forest 1995). In 1872 there were approximately 300 native Americans living at the Alsea sub-agency. Only 30 of these individuals were native Alsea, the rest were transplanted Coos, Kalapooyas and Umpquas (Hays 1976). In 1865 200,000 acres between the Alsea and Siletz rivers were removed from the Coast Range Reservation and opened to settlement (Siuslaw National Forest 1995). In 1875, Congress eliminated the entire southern portion of the Coast Range Reservation. At this point, the lands in the Cummins Creek area were officially opened for settlement.

Euro-American Settlement

The Homestead Act of 1862 offered up to 160 acres of public land to any individual who lived on and improved the land for a period of five years (Juntunen and Roberts 1994). The earliest homesteads in the Cummins Creek area were established under the provisions of this act, and were located along the relatively flat, coastal strip at the western edge of the present wilderness boundary (Figure 2). L. F. Cummings was the first to settle in the area. Beginning in 1884, he homesteaded on approximately 50 acres along the coastal strip in section 10. Frank Drew reported to John Harrington that the Cummins Creek area was "great wolf country", but that Cummings had left out poison to kill the wolves. The homestead of Allan H. Gwynn, established in 1892, appears to have encompassed most of the coastal strip in section 15, as well as some of the coastal land in section 22. Another early settler along the coastal strip was William F. Sharman, whose 160-acre homestead was established in 1900 and encompassed portions of sections 14, 15, and 22. In the early 20th century, W. H. Galvin established a homestead along Bob Creek in sections 14 and 23.

In 1907 the Siuslaw National Forest was created by a proclamation of President Theodore Roosevelt which added 16 million acres to the nation's forest reserves. Homestead applications in the early 20th century were filed under the Forest Homestead Act of 1906, which allowed homestead entry on forest reserve lands that had high agricultural value or were not needed for public purposes (Juntunen and Roberts 1994). Homestead claims filed under this act were well documented, and Forest Service records provide some information about homesteading in the Cummins Creek area. Thomas Collins initially occupied a homestead in section 14, but the claim was abandoned after 1909 following a crop failure. Wesley I. Watson, a veteran of the Spanish-American war, subsequently filed a claim on this land in 1911 and made homestead entry in 1915 (Figure 2). He died of unknown causes in 1917, and his widow, Charlotte A. Waston, left the homestead and moved to Yachats. Soon after, several individuals approached the Forest Service alleging that the land was abandoned and wishing to claim it for themselves. Upon learning that her claim was in jeopardy, Charlotte Watson returned to the homestead and patented it herself in 1918.

Another homestead was located on the western end of Tenmile ridge. This claim was filed in 1914 by John L. Baker, who made homestead entry along with his wife Mahala in 1915 (Figure 2). Shortly thereafter, Mahala divorced John to marry George M. Stonefield, who lived in the Tenmile Creek Valley. When Mahala asked John for the divorce, he reportedly replied that he "didn't give a damn" - arguably one of the more memorable quotes uttered by an inhabitant of the Cummins Creek area (Bogue and Yunker 1991). John Baker continued to live on the Tenmile Ridge homestead until the land was patented in 1921, but he abandoned it soon thereafter. He continued to use the land as a hunting camp until his death in the 1940's. Various remnants of the former settlement can still be found at the site, such as a

spring pooled with an earthen dam and a row of fence posts around a former pasture, now overgrown with alder.

Several unsuccessful homestead claims were filed on land in sections 11, 12 13, and 14. These claims encompassed land along the ridge between Cummins and Gwynn Creeks and the valley floor of Cummins Creek itself. These claims were rejected because of the small amount of relatively flat (< 25% slope) arable land, and because these areas contained areas of timber that the government wanted to maintain within the forest reserves. Rejected claims such as these often precipitated one or more appeals, and led to acrimonious conflict between would-be homesteaders and the Forest Service. It is not altogether clear whether the settlers attempting to claim these lands were simply naïve, or whether they were speculators trying to get hold of timberlands that they could later sell for a profit. In a description of one of the rejected claims, a Forest Service surveyor named J. Gribble mentioned that L. E. Dole, who had a ranch had on upper Big Creek, had written several articles in the Oregon Journal in 1914 and 1915 exaggerating the quality and availability of homestead land along the coast. These articles apparently deluded several potential homesteaders into filing claims on unsuitable land.

Most coastal homesteads were engaged in predominantly sustenance farming. A description of the John Baker homestead, for example, listed crops of hay, oats and strawberries along with a small garden and a few livestock. Farming of many crops was limited by the cool, moist summer weather along the coast. Poor travel routes also limited opportunities for commerce. The coastal highway during the late nineteenth and early twentieth centuries was nothing more than a dirt road. Many of the inland settlements could only be reached by trails that could not be traveled by wagons. One exception was the Stonefield Cattle Ranch, which encompasses nearly all the coastal land to the south of the

Cummins Creek Wilderness. Cattle raised here were sold commercially and driven each year to Cushing, where they were loaded onto railroad cars and shipped east to Eugene (Thompson 1986).

The settlers undoubtedly had a strong impact on forest vegetation along the coastal strip, on the headlands, and along the wide stream valleys where homesteads were most prevalent. Homesteaders often used fire to clear brush and other vegetation, along with dynamite to destroy the remnant snags and logs from the nineteenth century fires (Hays 1976, Thompson 1986, Bogue and Yunker 1991). Settlers also burned hillslopes for grazing, particularly the slopes of Fairview mountain just a few kilometers to the south of Cummins Creek. This burning started the Fairview Mountain fire of 1910, which burned hundreds of hectares in the Tenmile and Rock Creek watersheds (Bogue and Yunker 1991, Siuslaw National Forest 1995). Several homestead survey maps of the western boundary of the Cummins Creek wilderness also list some ridges as "burned in 1910", but it is not clear where these areas were part of the Fairview mountain fire or burned independently. In 1915, one surveyor describing a potential homestead site in the southwest portion of our study area noted that: "These ridges have burned over numerous times, which has killed nearly all young timber growth, so that now practically all there is left is brush of different kinds and alder coming along in the canyon bottoms." Although there is no direct evidence that settlers ignited these fires, is reasonable to assume that homesteaders in the Cummins Creek area used fire as a vegetation management tool. If burning occurred during the summer months, it is possible that the prevailing westerly winds could have carried the fires inland and burned portions of our study area.

Most of the coastal settlements were abandoned by the 1930's (Siuslaw National Forest 1995). The unsuitability of much of the land for agriculture combined with the relative

isolation of the area and transportation difficulties probably all played a role in the settlement failures. The Western Oregon Scattered Settlers Project was established under the New Deal to purchase small, scattered tracts of private land adjacent to the Siuslaw National Forest and to help train the dispossessed settlers for new jobs (Juntunen and Roberts 1994). In 1950, the John D. Baker homestead on Cummins Ridge was transferred to the federal government for the sum of $500. Most of the former homestead now lies within the Cummins Creek Wilderness. The former W. L. Galvin homestead also lies within the current wilderness boundaries, although the manner in which ownership returned to the Federal Government is unknown. Much of the former homestead land in sections 10 and 15 is currently owned by the State of Oregon, and comprises the Neptune State Park. Other former homesteads, such as the Watson property in section 14, remain in private ownership.

Current Human Uses

Although timber harvests from Federal lands had been minimal before World War II, they increased considerably starting in the 1950's (Siuslaw National Forest 1995). The amount of forests cut within the Cummins Creek Wilderness was considerably lower than in other coastal streams in the vicinity. Most of the timber harvest was concentrated in the Cape Creek (Lane County) drainage to the south, and the upper portions of the Big and Tenmile Creek basins. Cadastral land survey records indicate that the Cape Creek drainage supported one of the larger areas of old growth that had survived the 19th century fires (Dewberry 1984), and this may have been the reason why timber harvests were initially concentrated there. Cutting in the present-day Cummins Creek Wilderness was concentrated around the edges of the current wilderness boundary. Two small clearcuts were made in the interior of the Cummins

Creek drainage in the late 1970's. None of the federal land within the Bob Creek drainage has been cut, although some private land close to the coast has been harvested.

Cummins Creek was designated as a wilderness area by the Oregon Wilderness Act of 1984. The definition of a wilderness area, outlined in the Wilderness Act of 1964, states that:

> "A wilderness...is hereby recognized as an area where the earth and its community of life are untrammeled by man, where man himself is a visitor who does not remain. An area of wilderness is further defined to mean in this Act an area of undeveloped Federal land retaining its primeval character and influence, without permanent improvements or human habitation, which is protected and managed so as to preserve its natural conditions..."

As a result of the wilderness designation, the potential for resource extraction and development has been severely curtailed. The primary human use of the Cummins Creek Wilderness is currently non-motorized recreation (Siuslaw National Forest 1995). Recreational use appears to be quite low (1,200 visits per year), however, in comparison to some of the more popular nearby sites such as Cape Perpetua (> 30,000 visits per year). The recreational survey data probably does not include use by hunters who often do not enter the wilderness by established trailheads and do not fill out the survey forms. Little fishing appears to take place in Cummins of Bob creeks. Oregon Department of Fish and Wildlife records list no returned Coho or Steelhead tags for Cummins Creek in 1994.

Another important human use of the Cummins Creek Wilderness is as a research site, particularly for aquatic studies. Natural areas are often used as a baseline or "control" against which to compare other systems that have been more heavily impacted by humans (Franklin 1987). The Cummins Creek watershed, for example, has been contrasted against the more heavily harvested Cape Creek basin in studies of beaver affects on aquatic habitat (Bruner 1989) and salmonid community structure (Haapla 1998). Cummins Creek is also being used as a control against which to compare aquatic habitat restoration efforts in the Tenmile Creek

basin. The Little Cummins Creek watershed was compared with the Gwynn Creek and Cape Creek (Lincoln County) watersheds in a study of debris torrent impacts on channel morphology (Kaufmann 1988). The large amount of research in Cummins Creek has led to a proposal for the establishment of a Research Natural Area encompassing the Cummins and Gwynn Creek Watersheds (Siuslaw National Forest 1995).

Summary

Human perception and utilization of the Cummins Creek Wilderness has changed considerably over the past 200 years. The Alsea extracted resources from the forest on a limited basis, and did very little to modify the forest. Euro-American settlers, in comparison, took a more direct and aggressive approach to utilizing the land—converting former forestland to agriculture and burning other areas for grazing or by accident. Despite the ability of these settlers to modify the land, homesteading was ultimately unsuccessful. Human technology could not overcome the unsuitability of the climate for agriculture and the geographic isolation of the area. The area is highly suited to growing trees, however, and the homestead era was followed by an attempt to regulate and manage the coastal forests for wood production. This new vision of the landscape was ultimately thwarted by ecological concerns that led to the designation of wilderness areas such as Cummins Creek, and ultimately to the designation of the surrounding areas as a late-successional reserve as part of the Northwest Forest Plan (FEMAT 1993). In some ways, our current passive, low-intensity approach to managing these forests is similar to that of the native Alsea. Barring any radical changes in forest management legislation, the Cummins Creek Wilderness will provide a valuable location for recreation, research, and solitude for many years to come.

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