

HISTORIC AND SIMULATED VEGETATION DYNAMICS IN FORMER OREGON
WHITE OAK SAVANNA, SOUTHERN WILLAMETTE VALLEY, OREGON, USA

by

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THESIS ABSTRACT

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Doctor of Philosophy

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March 2012

Title: Historic and Simulated Vegetation Dynamics in Former Oregon White Oak Savanna, Southern Willamette Valley, Oregon, USA

Oak savanna was once widespread throughout the Willamette Valley, but changes in land use and disturbance regimes have degraded or destroyed most of that habitat. To identify how succession has operated in the past, I calculated tree growth rates. To assess the potential fire behavior in different successional communities, I collected data on vegetation and fuels, which I then used in a fire model. Finally, to project how succession may affect vegetation in the future and the potential for oak savanna conservation and restoration, I developed a new vegetation model that allows for projections of successional dynamics that are sensitive to change in climate, fire regimes, and human land-use and land-management decisions. Results highlight the complex and nuanced influences of environmental variables on successional trajectories and potential fire behavior. The novel vegetation model showed complex and plausible vegetation dynamics across a wide range of climate and disturbance scenarios.

This dissertation includes previously published and unpublished co-authored material.

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DEDICATION

כבוד את אביך ואת אמך

I dedicate this work to my parents

TABLE OF CONTENTS

Chapter	Page
I.	INTRODUCTION 1
	Dissertation Research..... 4
II.	ECOLOGICAL CONTROLS OF RECENT TREE GROWTH RATES IN CURRENT AND FORMER OREGON WHITE OAK SAVANNA IN THE WILLAMETTE VALLEY, OREGON, USA 7
	Introduction..... 7
	Material and Methods 9
	Results..... 14
	Discussion..... 19
	Conclusions..... 21
	Bridge to Chapter III..... 21
III.	ECOLOGICAL CORRELATES OF FUEL DYNAMICS AND POTENTIAL FIRE BEHAVIOR IN FORMER UPLAND PRAIRIE AND OAK SAVANNA 22
	Introduction..... 22
	Materials and Methods..... 24
	Study Areas 24
	Environmental Sampling Methods 26
	Fuel Sampling Methods 27
	Forest Cover Types 29
	Fire Behavior Modeling..... 29
	Statistical Analyses 31
	Results and Discussion 33
	Forest Cover Types 33
	Variation in Fuel Loads by Forest Cover Type 34
	Variation in Fire Behavior by Forest Cover Type 37

Chapter	Page
Fire Behavior Community Types – Surface Fire Intensity	39
Fire Behavior Community Types – Crown Fire Initiation.....	43
Conclusions.....	45
Bridge to Chapter IV.....	48
IV. A NEW MODELING APPROACH FOR PROJECTING CLIMATE CHANGE IMPACTS ON FOREST SUCCESSION FOR LOCAL LAND MANAGEMENT.....	50
Introduction.....	50
Model Design.....	52
Spatial Framework	52
Plant Community Definitions	54
Transition Probability Initialization	54
Transition Probability Modifications and Emergence of Novel Communities.....	55
Design Summary.....	56
Study Area.....	57
Model Parameterization	59
State and Transition Model	59
Transition Probability Initialization	61
Transition Probability Adjustments and Constraints	62
MC1 Customization.....	62
MC1 Future Projections.....	64
Transition Probability Adjustments	66
Transition Probability Constraints	67
Model Behavior	69
STM Probabilistic Behavior	69
Effects of Disturbance and Climate Change.....	70
Spatial Output	75

Chapter	Page
Discussion.....	76
Conclusions.....	83
V. CONCLUSIONS.....	85
Summary of Major Results	85
Implications for Studying and Modeling Successional Dynamics	87
APPENDIX: SUPPLEMENTAL MATERIALS TO CHAPTER IV	90
S1. CO ₂ Parameterization Experiments	90
S2. STM Cover Type Descriptions	92
S3. R Code to Run CV-STM Outside of Envision.....	94
REFERENCES CITED.....	98

LIST OF FIGURES

Figure	Page
2.1. Study Sites within the Willamette Valley Ecoregion, Oregon, USA	9
2.2. Boxplot of Absolute Growth Rate by Species and Site	16
3.1. Location of the Willamette River Basin within Oregon, USA	25
3.2. Ordination of Plots by Plant Community Variables.....	30
3.3. Plots of Fuel Loads by Forest Cover Type.....	35
3.4. Plots of Fuel Structure by Forest Cover Type.....	36
3.5. Plots of Heat-per-unit-area and Crown Fire Transition Ratio by Forest Cover Type.....	38
3.6. CART Analysis of Heat-per-unit-area.....	40
3.7. CART Analysis of Heat-per-unit-area for “Prairie, Savanna and Woodland from Figure 3.6.....	41
3.8. CART Analysis of Crown Fire Transition Ratio.....	44
4.1. Schematic Diagram of CV-STM Coupled with MC1, FVS, and Envision.....	53
4.2. Study Area Location in the Willamette Valley, Oregon, USA	58
4.3. Elevation for the Study Area.....	58
4.4. The Dynamic Global Vegetation Model MC1 Potential Vegetation Types at Year 0 (2007) and Year 90 (2097) under the Hadley A2 Global Circulation Model	65
4.5. Changes in State-and-Transition Model Cover Types over Time.....	71
4.6. Projected STM Cover Types in Number of Integrated Decision Units at Four Time Points with Three Global Circulation Models.....	73
4.7. Extent of Ponderosa Pine Cover Types.....	74
4.8. Simulated Plant Cover Types Shown Spatially for the Study Area	76
S1. Aboveground NPP over Time	91

LIST OF TABLES

Table	Page
2.1. Site Name, Latitude, Longitude and Elevation Range for the Study Sites	10
2.2. Number of Trees Sampled at Each Site, by Species Used in this Analysis	12
2.3. Mean Absolute Growth Rate by Species Across all Sites.....	14
2.4. Pearson’s Correlation Coefficient Between Size-and-Age Standardized Radial Growth Increment and Environmental Variables	18
3.1. Site Name, Latitude, Longitude and Elevation Ranges of the Study Sites.....	27
3.2. Variables Used in this Study	28
3.3. Ranges of Crown Fire Transition Ratio Values in the Categories used for CART Analysis	34
4.1. State-and-Transition Model Tree Cover Types with Dominant and Associated Local Species.....	60
4.2. Variables Used in the Regression Equation Relating MC1 Variables to Site Index	67
4.3. State and Transition Model Tree Cover Types to which Transitions Are Allowed under each MC1-Derived Potential Vegetation Type.....	68
S1. Parameterization of co2itr and co2ipr to Achieve Different Levels of CO ₂ Fertilization in MC1.....	90
S2. Live Tree Carbon from Three Points in the Study Area in 2007	91

CHAPTER I

INTRODUCTION

Savannas occur across a variety of climatic zones (Köppen, 1923), from the tropics to boreal regions, from low to high elevations, and from xeric to mesic sites. Indices of solar radiation and aridity are generally predictive of the broad, but not local, distributions of savanna (Budyko, 1963). Within areas demarcated as savanna, for example, minor differences in soils can lead to changes from prairie to shrubland to savanna to forest (Lapin and Barnes, 1995). There is adequate soil moisture to support dense forests in many areas that currently are, or historically were, savanna, so the maintenance of these ecosystems is often dependent on disturbance, whether that disturbance is fire, freezing, or grazing (Groom and Vynne, 2006). Human alteration of these disturbance regimes often leads to degradation of savanna ecosystems, as documented in Asia (Singh and Joshi, 1979), Australia (Walker and Gillison, 1982), Africa (van Vegten, 1984), South America (Schofield and Bucher, 1986), Europe (Bugalho et al., 2011), and North America (White et al., 2000; Groom and Vynne, 2006). As a result of these and other perturbations, savanna ecosystems are in decline globally (White et al., 2000).

The low-elevation inland valleys of western Oregon and Washington are a useful case of study of these broader trends. Oregon white oak (*Quercus garryana* Dougl.) savanna was once a dominant habitat type from the Puget Trough in the north through the Willamette Valley, and to northern California in the south (Habek, 1961; Thilenius, 1968; Agee, 1996; Walsh, Pearl, et al., 2010; Walsh, Whitlock, et al., 2010). Oak savanna expanded into this region following the last glacial maximum, approximately 14,000 years before present (Whitlock, 1992). The distribution of Oregon white oak savanna reached its peak 10,000 to 7,000 years before the present, and was the dominant vegetation type in valleys and up to 500 m elevation in the Coast and Cascade Ranges (Sea and Whitlock, 1995; Walsh, Pearl, et al., 2010). Prior to Euro-American settlement, Oregon white oak savanna still occupied approximately 219,000 ha in the Willamette Valley (Hulse et al., 2002; Christy and Alverson, 2011). Most of this habitat has been lost

due to changes in the fire regime, land-use and land management (Hulse et al., 2002). In this regard, the Willamette Valley is similar to other regions of North America, where the distribution of oak savanna increased following the last glacial maximum, and then decreased sharply following Euro-American settlement (Noss et al., 1995).

Ecological restoration is the assisted recovery of degraded, damaged or destroyed ecosystems (Society for Ecological Restoration International Science & Policy Working Group, 2004), and the frequency and spatial extent of restoration projects are increasing rapidly (Higgs, 2003). While some forms of restoration likely date back thousands of years (Black et al., 2006), modern restoration began with Aldo Leopold in the early 20th century (Meine, 1991). Most successful restoration projects target ecosystem processes (Fiedler and Groom, 2006), like disturbance, rather than attempting to directly achieve a desired community. This focus on ecosystem processes recognizes that ultimately ecological succession will determine which communities of species will persist in a given habitat over time (Higgs, 2003).

Ecological succession is the change in community composition over time (Clements, 1916; Gleason, 1917). Ecological succession can be a rapid process (Olson, 1958) that does not necessarily follow a prescribed order (Beisner et al., 2003). Across a landscape with a mosaic of disturbance regimes and diverse species, many species may be able to coexist dynamically (Schröder et al., 2005). As climate changes globally, successional changes may accelerate as native and exotic species invade new habitats (Stachowicz et al., 2002; Ward and Masters, 2007). Species' individual capacities to adapt to changing climate (Bradshaw and Holzapfel, 2006) may also affect successional trajectories.

There are a number of key factors that control the success of different tree species over the course of ecological succession. For tree species, differences in their capacity to germinate in a variety of conditions contribute to their competitive success. Douglas-fir (*Pseudotsuga menziesii* Mirb.) requires bare mineral soil for germination, whereas grand fir requires a developed duff layer (Sprague and Hansen, 1946; Heit, 1968). Douglas-fir also prefers moderate insolation for germination, while grand fir (*Abies grandis* Dougl.) prefers low insolation for germination. Oregon white oak prefers mineral soil, and is the most tolerant of high insolation for germination (Stein, 1990). In these ways, alternative

germination strategies contribute to the differential reproductive success of competing tree species, which in turn contributes to typical successional trajectories. Between trees of different species, water use efficiency, optimal light wavelength and intensity (Huston and Smith, 1987), secondary metabolic compounds (Swain, 1977), belowground chemistry and interactions with microbial communities (Casper, 1997), among other physiological characteristics, also contribute to determining which individual trees and tree species are most successful in a particular competitive environment.

The spatial and temporal heterogeneity of disturbances is also a central factor in creating the dynamic landscapes that we observe today. In terrestrial systems, important biologically-mediated disturbances include insect defoliation (Kulman, 1971), herbivory (Hairston et al., 1960), bioturbation (Bond, 1945), and, of course, harvest of biomass by humans (Sohnngen and Sedjo, 2000). Abiotic disturbances include geologic activity and storm damage. Disturbance by fire may be unique in its combination of biological and abiotic origin (Bond et al., 2005). Organisms show adaptations to different disturbance regimes (Lytle and Poff, 2004), and disturbance regimes strongly affect species diversity (Grime, 1973).

Fire is among the most important agents of disturbance globally for terrestrial ecosystems (Bond, 1996). As with other disturbance types, many species show adaptation to particular fire regimes (Mutch, 1970; Bond and Midgley, 1995). Fire interacts with climate change (Bond et al., 2005; Gavin et al., 2007; Rogers et al., 2011) and changes in human land use (Foley et al., 2005). As human population continues to expand into areas of flammable vegetation, understanding potential fire behavior becomes increasingly important (Yospin et al., 2012).

Climate has been changing throughout the history of the Earth, but changes are now primarily driven by human greenhouse gas emissions and changes in land use and land cover (IPCC, 2007a). Many extant plant communities established under climate that is markedly different from today's (Briles et al., 2005), such as the Little Ice Age from c. 1500-1800 AD (Matthes, 1939). Understanding successional dynamics in the future will require not only an understanding of these historical changes in climate and vegetation, but also computer models that can mechanistically simulate the interactions of climate and vegetation, especially as mediated by changing fire regimes.

The most widely accepted way to explore the potential future interactions of climate change, succession, and disturbance relies on dynamic global vegetation models (IPCC, 2007b). Research has been conducted using models that operate in slightly different ways for various regions at various scales. Some important examples of this work include simulations of vegetation dynamics within North America with MC1 (Bachelet et al., 2003), ED2 (Medvigy et al., 2009), Biome-BGC and Century (Schimel et al., 2000), IBIS (Kucharik et al., 2000), and LPJ (Sitch et al., 2003). In particular, MC1 has been parameterized for and used in the Pacific Northwest (Bachelet et al., 2011; Rogers et al., 2011). Despite these extensive and useful research efforts, new modeling tools are necessary to explore potential future vegetation dynamics at the extremely fine spatial and temporal scales where land-use and land-management decisions are made.

Dissertation Research

This dissertation describes work that documents the role of environmental variables in controlling successional trajectories in current and former Oregon white oak savanna in the Willamette Valley, Oregon, USA. To identify how succession has operated in the past, I collected field data and calculated tree growth rates. To assess the potential fire behavior in different successional communities, I collected field data on vegetation and fuels, which I then used in a fire model. Finally, to project how succession may affect vegetation in the future, and the potential for oak savanna conservation and restoration, I developed a new vegetation model that allows for projections of successional dynamics that are sensitive to change in climate, fire regimes, and human land-use and land-management decisions.

The title of Chapter II is “Ecological controls of recent tree growth rates in current and former Oregon white oak savanna.” This chapter is being prepared for submission to *Northwest Science*, and is co-authored with Daniel G. Gavin, Scott D. Bridgham, and Bart R. Johnson. For this study, we sought to document the stand histories and growth rates of the dominant tree species in current and former Oregon white oak savanna in the southern Willamette Valley. Information on the growth of tree species in current and former Oregon white oak savanna will benefit conservation and restoration of this critically imperiled ecosystem. We collected data on soils, topography, and plant

communities from plots at seven sites in the southern Willamette Valley. We also collected increment cores from trees, and used these cores to measure recent tree growth rates. Using ANOVA and regression, we analyzed the relationship among environmental variables and tree growth rates.

The title of Chapter III is “Ecological correlates of fuel dynamics and potential fire behavior in former upland prairie and oak savanna.” This chapter is published in *Forest Ecology and Management*, and is co-authored with Scott D. Bridgham, Jane Kertis, and Bart R. Johnson (Yospin et al., 2012). In this study, we sought to identify potential fire behavior in former prairie and savanna following forest succession. We also explored the use of plant community data to predict potential fire behavior. If plant community data could be used to predict wildland fire behavior, land managers could use this information to more quickly and inexpensively estimate potential fire behavior for lands with diverse successional histories. We collected data on fuel loads from the same study plots we used for Chapter II. We defined eight forest cover types; an ordination based on tree species basal area by diameter classes and the cover of ground layer functional types supported these community types. We first calculated and compared fuel loads for each community type. We then used a fire behavior model, BehavePlus, to simulate potential fire behavior in our study plots. Because plant community data, standard fuel models and the ordination axes were poor predictors of fuels and potential fire behavior, we explored a new method of incorporating ecological data into predictions of fire behavior. We used classification and regression trees (CARTs) to find groups of plots that differed in their potential fire behavior.

Chapter IV, “Projecting climate impacts on forest succession for local land management,” describes the intellectual and technical development of a new vegetation model, Climate-Sensitive Vegetation State-and-Transition Model (CV-STM). Our goal was to build a model that could simulate species-specific successional trajectories and their changes in response to changing climate and human management. Because fire has been, is, and will be a major agent of disturbance in this region, the vegetation model will interact with a mechanistic fire model. To meet all of these goals, the new model therefore had to be spatially explicit. The vegetation model that emerged from this work achieves all of these goals, and is a major and novel contribution to the field. We tested

this new model across a wide range of future climate and disturbance scenarios to assess its performance. This chapter is being prepared for submission to *Global Change Biology*, co-authored by Scott D. Bridgham, John P. Bolte, Ronald P. Neilson, Dominique Bachelet, Peter Gould, Connie Harrington, Jane Kertis, James Merzenich, Cody Evers, and Bart R. Johnson.

In Chapter V, I summarize the results of the original research presented in Chapters II through IV. I conclude with suggestions on how my work suggests future directions for research at the interface of ecology, computer modeling, and land management policy.

CHAPTER II

ECOLOGICAL CONTROLS OF RECENT TREE GROWTH RATES IN CURRENT AND FORMER OREGON WHITE OAK SAVANNA IN THE WILLAMETTE VALLEY, OREGON, USA

A paper in preparation for submission to *Northwest Science*, co-authored with
Daniel G. Gavin, Scott D. Bridgham, and Bart R. Johnson

Introduction

Within climatically similar regions, spatial differences in tree growth rates are controlled by soils (Gower et al., 1996; Ryan and Yoder, 1997), topography (Callaham, 1962; Roy et al., 1999), disturbance (Canham, 1988; Bond, 1996; Kaitaniemi et al., 1999), competition (Leak, 1975), and successional history (Brokaw and Busing, 2000). Understanding these environmental controls over growth rates for individual tree species is central to predicting the outcomes of interspecific competition and successional trajectories.

Former *Quercus garryana* (Dougl.) savanna provides a useful system for studying how environmental controls over individual tree growth rates translate into alternative successional trajectories across a landscape. Prior to Euro-American settlement in western Oregon (circa 1840), *Q. garryana* savanna was the dominant oak community type (Thilenius, 1968), occupying over 219,000 ha, or 17% of the Willamette Valley Ecoregion (Hulse et al., 2002). Most *Q. garryana* are now in dense woodlands and forest (Hulse et al., 2002), frequently in different types of mixed coniferous-broadleaf stands (Gilligan and Muir, 2011), and often in declining health and abundance due to competition from overtopping Douglas-fir (Clements et al., 2011). This diversity of outcomes following 170 years of succession serves as a natural experiment, which we use here to explore the causes and consequences of differential tree growth at the landscape scale.

Preserving and restoring *Q. garryana* savanna has recently emerged as a top regional conservation priority (MacDougall et al., 2004; Ulrich, 2010; Michalak, 2011).

These habitats are valuable in terms of biodiversity (Wilson and Carey, 2001; Altman, 2011) and ecosystem services, such as fire regime regulation (Yospin et al., 2012). It is widely accepted that *Q. garryana* savannas were maintained as a dominant ecosystem throughout much of the valley lowlands of the western Pacific Northwest for millennia due to natural and anthropogenic fire (Morris, 1934; Thilenius, 1968; Walsh et al., 2010), to which *Q. garryana* is well-adapted (Agee, 1996; Bond, 1996). Since the mid-1800s however, the alteration of historical fire regimes has allowed large increases in tree density and increasing conifer dominance (Agee, 1996; Foster and Shaff, 2003; Day, 2005). Coupled with large habitat losses due to agriculture and urbanization, this once abundant ecosystem has now become rare (Hulse et al., 2002).

Tree growth is one of the best indicators of the suitability of a site for conservation or restoration (Gould et al., 2011), especially when desired characteristics include large and long-lived trees (Poage and Tappeiner, 2002). To satisfy the growing desire to make informed decisions about *Q. garryana* savanna conservation and restoration, it is necessary to identify environmental controls over the growth of the dominant tree species in these ecosystems. There is still debate, however, over the history, maintenance requirements and successional dynamics of *Q. garryana* savanna (Agee, 1996; Hosten et al., 2006; Gilligan and Muir, 2011). Possible explanations for areas of remnant *Q. garryana* savanna include recent disturbance and limiting edaphic conditions such as shallow soil depth (Thilenius, 1968; Hosten et al., 2006; Murphy, 2008). Stand density and canopy position strongly affect the growth and survival of *Q. garryana* (Gould et al., 2011), so environmental factors that reduce competition from other tree species often maintain *Q. garryana* savanna (Maertens, 2008). An understanding of these factors should improve our ability to predict *Q. garryana* growth and survival, and to choose suitable sites for conservation and restoration.

To better understand the mechanisms underlying the spatial and temporal patterns of forest succession on current and former oak savanna, we analyzed the recent growth rates of six dominant tree species in relation to soils, topography and plant communities on seven sites with former oak savanna in various stages of forest succession. While stand history reconstructions of *Q. garryana* ecosystems have helped elucidate successional dynamics (Day, 2005; Gedalof, 2006; Dunwiddie et al., 2011; Gilligan and

Muir, 2011), to our knowledge, no study of these dynamic ecosystems, with their complex histories of disturbance and land use, has comprehensively compared growth rates among the dominant tree species to environmental variables.

Materials and Methods

We established 182 plots at seven sites in the southern Willamette Valley, Oregon (Figure 2.1).

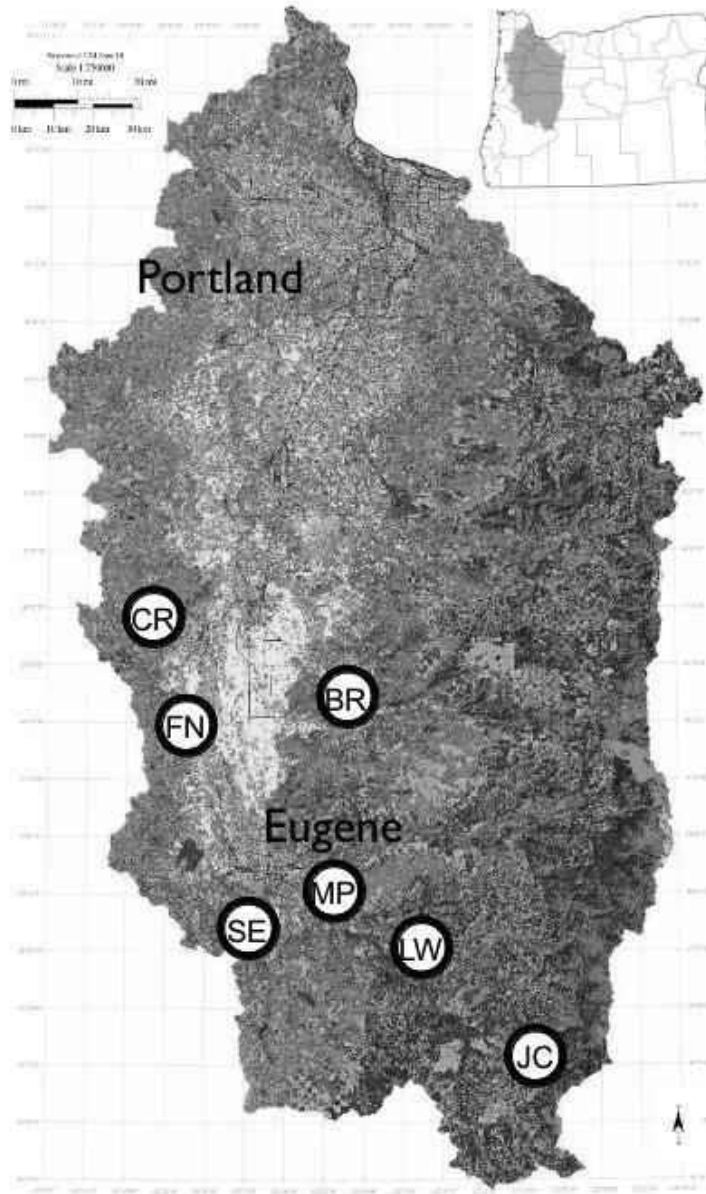


Figure 2.1. Study sites within the Willamette Valley Ecoregion, Oregon, USA. Modified from (Hulse et al., 2002).

We confirmed that all plots were located in former savanna by viewing the study sites in ArcGIS (ESRI, 2009) using a map of vegetation c. 1851 (Pacific Northwest Ecosystem Consortium, <http://www.fsl.orst.edu/pnwerc/wrb/access.html>). Sites locations ranged from the valley floor (Finley), to buttes within the valley (Chip Ross, Mount Pisgah, and South Eugene), to the foothills of the Cascade Mountains (Lowell, Brownsville, and Jim's Creek). Plots at Finley had the lowest elevations in our study (85 m), while Jim's Creek had the highest (988 m), with the other five sites filling in the elevation gradient between these two (Table 2.1). Areas within sites that had been significantly disturbed within the last 25 years prior to data collection were excluded at the time of plot selection. Soils in all sites were Mollisols, Inceptisols and Ultisols.

Table 2.1

Site name, latitude, longitude and elevation range for the study sites.

Site	Latitude	Longitude	Elevation Range (m)	Number of plots	Soil Orders
Finley	44°25'N	123°19'W	85 - 165	41	Ultisol, Inceptisol, Mollisol
Chip Ross	44°34'N	123°16'W	183 - 259	25	Mollisol, Inceptisol, Mollisol, Inceptisol,
Mount Pisgah	44°00'N	122°58'W	171 - 347	18	Ultisol
South Eugene	44°03'N	123°06'W	201 - 347	18	Mollisol, Inceptisol
Lowell	43°55'N	122°46'W	305 - 488	24	Mollisol, Inceptisol, Mollisol, Inceptisol,
Brownsville	44°23'N	122°59'W	183 - 610	13	Ultisol
Jim's Creek	43°30'N	122°25'W	597 - 988	43	Inceptisol

Stratified random belt transects were established at each study site, oriented up and down slopes, to span important changes in topography and plant communities. Plots were located every 30 m along these transects. The number of transects varied among sites, and the lengths of transects varied within sites, in order to encompass the variation in plant communities and environments present; therefore each site had a different

number of plots (Table 2.1). Species and diameter at breast-height (DBH) categories (<12, 12-25, >25-50, >50-75, >100 cm) were recorded for every tree within 8 m of the plot center. We measured percent slope using a clinometer, averaging one measurement up-slope with one measurement down-slope. We recorded the dominant aspect of the plot using a compass. This information allowed us to calculate heat load for each plot (McCune and Keon, 2002). Four measurements of tree canopy cover, between July and September, were taken with a spherical densiometer (Lemmon, 1956). We recorded percent cover of the ground layer, shrubs, forbs, graminoids and moss by ocular estimation (Braun-Blanquet, 1932; Daubenmire, 1959).

Soil depth-to-obstruction was measured for nine points in each plot using a battery-powered drill and a 0.3-cm diameter steel rod. We composited three random soil samples for each plot, from 0-5 cm depth using a bulb planter, and from 5-20 cm depth using an Eigelkamp soil auger (Murphy, 2008). We composited ten random O-horizon samples for each plot using a bulb planter. We measured soil pH in a 1:1 soil-water slurry. Clay content was determined with a modified hydrometer method of Gee and Bauder (Gee and Bauder, 1986; Gavlak et al., 2003). We isolated sand with a 53- μ m sieve, and then oven-dried (60 °C) and weighed it; percent silt was determined by subtracting %clay and %sand from 100. We determined total carbon and nitrogen levels with a Costech Analytical CN analyzer (Valencia, CA, USA). Finally, we assessed the dates and types of disturbances experienced by each plot using historic air photos beginning with the first available air photos (1936 or 1940) until 1978 (after which plots had not been significantly disturbed) at 10 year intervals (H. Wu and B. Johnson, unpublished data). We used the years elapsed since the last intensive disturbance of each plot as an explanatory variable for this study.

We collected tree cores in each plot from May to November of 2005, 2006 and 2007. We selected two trees from each species x DBH group that was present within 8 m of the plot center. Trees were cored once parallel to the contour of the slope, 0.8 m above the ground. Cores were processed using standard procedures (Stokes and Smiley, 1968). We counted annual growth rings for all samples to determine the age of each tree. We measured the widths of annual growth rings from 1990 until the last year of growth for all trees using a sliding-scale micrometer. For trees that were likely to have established prior

to Euro-American settlement c. 1850, we measured all the annual growth rings. When the core did not intersect the pith of the stem, we estimated the number of growth rings to the pith using the curvature and width of the innermost ring. Altogether, we cored, estimated age and measured decadal growth for 775 trees. These included 11 *Abies grandis*, 73 *Acer macrophyllum*, 39 *Calocedrus decurrens*, 32 *Pinus ponderosa*, 288 *Pseudotsuga menziesii*, 306 *Quercus garryana*, and 3 *Quercus kelloggii*. The small sample sizes of *A. grandis* and *Q. kelloggii* preclude analysis and discussion in text; without those two species, this data set represents 738 trees (Table 2.2). The abundances of each tree species varied substantially by site, leading to large differences in sample sizes. *Acer macrophyllum* was abundant at Finley and Mt. Pisgah; *Calocedrus decurrens* was abundant at Lowell and Jim's Creek. *Pinus ponderosa* was abundant at Jim's Creek; *Pseudotsuga menziesii* was abundant at Chip Ross, South Eugene, Brownsville, and Jim's Creek; and *Quercus garryana* was abundant at all sites.

Table 2.2

Number of trees sampled at each site, by species used in this analysis.

Site	<i>Acer macrophyllum</i>	<i>Calocedrus decurrens</i>	<i>Pinus ponderosa</i>	<i>Pseudotsuga menziesii</i>	<i>Quercus garryana</i>	Total
Finley	21	0	0	13	70	104
Chip Ross	5	0	0	47	68	120
Mount Pisgah	21	0	0	13	44	78
South Eugene	2	0	11	46	34	93
Lowell	11	16	1	15	54	97
Brownsville	13	0	1	24	17	55
Jim's Creek	0	23	19	130	19	191
Total	73	39	32	288	306	738

We used both COFECHA (Holmes, 1983) and R (R Development Core Team, 2008), library dplr (Bunn, 2010), to crossdate the cores. We used the absolute growth rate

(basal area growth increment: mm^2 per 10 years, calculated from the radial growth increment and DBH) to analyze differences in tree growth by species both across sites and within sites.

First, we analyzed absolute growth rate by species across all study sites. We used two-way ANOVAs to test for differences in growth by species, site, and the interaction between species and site. Because there was a significant interaction between site and species, we tested for differences in growth rate among sites for each individual species with a one-way ANOVA, and if this was significant, tested for pairwise differences using Tukey's HSD. We then constructed linear regression models for absolute growth rate across all sites by forward addition and backward elimination, and selected models that minimized Akaike's Information Criterion (AIC: Akaike, 1974).

Second, we analyzed finer-scale patterns in growth among plots within sites. To do this, we removed the site-wide effect of tree age and size, which are first-order controls on absolute growth (Gavin et al., 2008). We calculated the standardized radial growth index (SRGI) for each tree by dividing the observed radial growth increment (mm per 10 years) by the growth increment predicted using a LOESS regression (Cleveland, 1979) that controls for the effects of age and stem diameter. This LOESS regression, fit to each species at each site, predicts radial growth increment from tree diameter, log-transformed tree age, and the interaction of tree diameter and log-transformed tree age. This standardization results in a normally distributed dimensionless growth index. Because SRGI is generated independently for each site, it is not meaningful to examine SRGI except on a site-by-site basis. We then checked for correlations between environmental variables and SRGI, for each species at each site. When correlations between SRGI and environmental variables were at least marginally significant ($p > 0.10$), we constructed linear regression models as described above, confirming beforehand that explanatory variables were not strongly collinear, and that residuals were normally distributed. Because we used a nearly-exhaustive approach to selecting a regression model, we report adjusted r-squared values (r^2_{adj}). A model constructed using a single explanatory variable may therefore have a reported r^2_{adj} that is not equal to the square of the correlation coefficient for that variable.

Results

To compare growth rates, we focused only on the total growth of the most recent decade that all of the cores shared: 1995-2004. Crossdating verification statistics (not presented) were poor because of both the complicated interactions between disturbance and environmental conditions (see below) and because of very narrow growth rings in *Q. garryana*. Thus, the short segments measured on several cores precluded high interseries correlations. However, other work (Poage and Tappeiner, 2002; Maertens, 2008) indicates that missing and false rings are extremely unlikely in these species for this time period. Further, other research also indicates that the differences between cross-dated cores and well-prepared cores was only 1.5 years on average for *P. menziesii* cores that had approximately 400 years of growth (Weisberg and Swanson, 2001). For these reasons we believe that our measurements of decadal growth and tree age are reasonably accurate.

Table 2.3

Mean absolute growth rate by species across all sites.

Species	N	Mean Absolute Growth Rate	
		(mm ² per 10 years)	Standard Deviation
<i>Abies grandis</i>	11	230.74	329.32
<i>Acer macrophyllum</i>	73	136.18	128
<i>Calocedrus decurrens</i>	39	150.7	192.15
<i>Pinus ponderosa</i>	32	216.36	204.3
<i>Pseudotsuga menziesii</i>	310	167.05	194.09
<i>Quercus garryana</i>	306	145.2	214.38
<i>Quercus kelloggii</i>	3	192.10	271.11

Average absolute growth rate varied among sites ($F(6,744) = 3.06$, $p = 0.006$) but not by species ($F(6,744) = 1.51$, $p = 0.173$, Table 2.3), although the effect of site depended on species ($F(17,744) = 1.95$, $p = 0.012$, Figure 2.2). The only species that had

significant differences in growth rates across sites was *Q. garryana* ($F(6,299) = 4.11$, $p < 0.001$). Absolute growth rates were significantly greater at Finley than at Mount Pisgah ($p = 0.03$). Growth of *P. menziesii* differed across sites ($F(6,303) = 3.28$, $p = 0.004$), but there were no significant pairwise differences. Absolute growth rate did not differ across sites for the other species. It was possible to build two significant regression models across all sites using absolute growth rate. The first was for *Q. garryana* growth, using time since disturbance, with an overall $r^2_{\text{adj}} = 0.083$. The second was for *P. menziesii* growth using heat load and plot basal area ($r^2_{\text{adj}} = 0.072$).

Because these models explained so little variance, we proceeded to examine growth at the site level using SRGI (i.e., after first removing the mean effect of tree size and age on growth rate). The variance in radial growth increment explained by loess regressions with tree size and age was between 9% (for *P. menziesii* at Jim's Creek) and 52% (for *Q. garryana* at Chip Ross). In general, size and age explained about 20% of the variance in radial growth increment. For the purposes of this study, species-by-site combinations that had at least one correlation between SRGI and an environmental variable with a p -value > 0.10 are described in the text and listed in Table 4. There were no significant correlations between either *C. decurrens* SRGI or *P. ponderosa* SRGI and environmental variables.

Acer macrophyllum SRGI at Finley correlated significantly with percent nitrogen ($r = -0.44$) and percent carbon ($r = -0.38$), and was marginally correlated with time since disturbance ($r = -0.33$) (Table 2.4). Marginally significant regression models at Finley for *A. macrophyllum* SRGI used percent nitrogen ($r^2_{\text{adj}} = .15$, $p = 0.060$), and percent nitrogen and percent carbon ($r^2_{\text{adj}} = .16$, $p = 0.10$). At Mount Pisgah, *A. macrophyllum* SRGI correlated significantly with percent carbon ($r = 0.37$), and correlated marginally with plot basal area ($r = -0.35$) and elevation ($r = -0.36$). No significant regression model could be constructed for *A. macrophyllum* SRGI at Mount Pisgah.

Basal Area Growth Increment by Site and Species

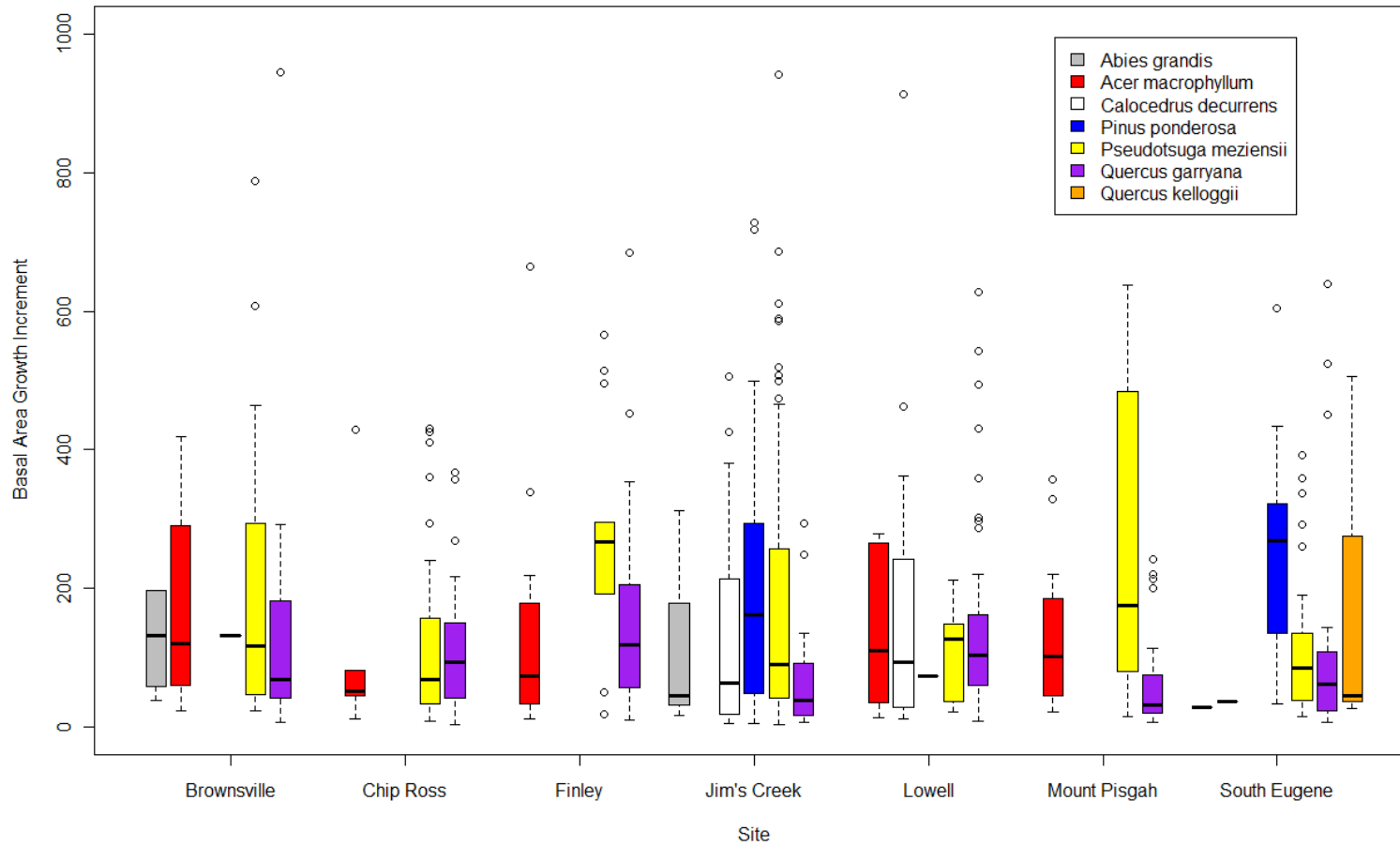


Figure 2.2. Boxplot of absolute growth rate by species and site. Species are shown nested within sites. Not all species were present at each site. Dark horizontal lines indicate group medians. Boxes contain the second and third quartiles of the distribution. Whiskers extend one interquartile distance beyond the boxes, and data that exceed the whisker are plotted as open circles

Pseudotsuga menziesii SRGI at Brownsville correlated significantly with time since disturbance ($r = -0.29$), and marginally correlated with percent nitrogen ($r = 0.28$). At Chip Ross, *P. menziesii* SRGI was significantly correlated with percent clay ($r = 0.28$). At Finley, *P. menziesii* SRGI was significantly correlated with heat load ($r = 0.53$). At Lowell, *P. menziesii* SRGI was significantly correlated with percent carbon ($r = -0.45$), and marginally correlated with percent nitrogen ($r = -0.42$) and soil pH ($r = -0.40$). At Mount Pisgah, *P. menziesii* SRGI was significantly correlated with percent nitrogen ($r = -0.56$), percent carbon ($r = -0.57$), and percent silt ($r = -0.62$), and marginally correlated with heat load ($r = 0.45$). At South Eugene, *P. menziesii* SRGI was significantly correlated with time since disturbance ($r = 0.30$). The only significant multiple regression for *P. menziesii* SRGI was at South Eugene ($r^2_{\text{adj}} = 0.07$, $p = 0.042$), using only time since disturbance as an explanatory variable.

There were more significant correlations between *Q. garryana* SRGI and environmental variables than for the other tree species (Table 2.4). At Chip Ross, *Q. garryana* SRGI was significantly correlated with percent nitrogen ($r = 0.23$), percent silt ($r = 0.22$), elevation ($r = -0.24$), and heat load ($r = -0.37$), and marginally correlated with percent carbon ($r = 0.17$). A multiple regression for *Q. garryana* SRGI at Chip Ross was significant ($r^2_{\text{adj}} = 0.17$, $p = 0.006$), using percent silt and heat load. At Finley, *Q. garryana* SRGI was significantly correlated with soil pH ($r = -0.28$), and marginally correlated with percent canopy cover ($r = 0.19$). A multiple regression for *Q. garryana* SRGI at Finley was significant ($r^2_{\text{adj}} = 0.10$, $p = 0.045$), using soil pH and canopy cover. At Jim's Creek, *Q. garryana* SRGI was significantly correlated with soil pH ($r = 0.50$), and percent nitrogen ($r = 0.50$), percent carbon ($r = 0.52$), percent clay ($r = 0.68$) and percent silt ($r = -0.53$). However, no regression models were significant for Jim's Creek. At Lowell, *Q. garryana* SRGI was significantly correlated with soil pH ($r = -0.26$), but no regression models were significant at this site. At Mount Pisgah, *Q. garryana* SRGI was significantly correlated with soil pH ($r = 0.26$), percent canopy cover ($r = 0.29$), heat load ($r = -0.31$), and time since disturbance ($r = -0.34$), and marginally correlated with plot basal area ($r = 0.25$). No regression models were significant for this site.

Table 2.4.

Pearson's correlation coefficient between size-and-age standardized radial growth increment and environmental variables for *Acer macrophyllum*, *Pseudotsuga menziesii*, and *Quercus garryana* at sites with at least one marginally significant correlation coefficient. ** $p < 0.05$, * $p < 0.10$. BR = Brownsville, CR = Chip Ross, FN = Finley, JC = Jim's Creek, LW = Lowell, MP = Mount Pisgah, SE = South Eugene.

Variable	<i>Acer macrophyllum</i>		<i>Pseudotsuga menziesii</i>				<i>Quercus garryana</i>						
	FN	MP	BR	CR	FN	LW	MP	SE	CR	FN	JC	LW	MP
Soil Depth	-0.13	-0.22	-0.25	0.15	NA	-0.03	0.15	0.05	0.01	0.02	0.18	-0.01	0.07
Soil pH	-0.26	0.05	0.01	-0.05	0.29	*-0.40	-0.38	0.09	-0.07	**0.28	**0.50	**0.26	**0.26
% Nitrogen	**0.44	0.30	*0.28	-0.04	-0.22	*-0.42	**0.56	0.00	**0.23	-0.04	**0.50	0.04	0.00
% Carbon	**0.38	**0.37	0.14	-0.09	-0.20	**0.45	**0.57	-0.01	*0.17	0.00	**0.52	0.05	0.09
% Clay	-0.05	-0.27	0.05	**0.28	0.14	-0.10	-0.19	0.01	-0.12	-0.06	**0.68	0.01	0.02
% Silt	-0.04	0.15	0.20	-0.02	-0.06	0.03	**0.62	0.00	**0.22	0.05	**0.53	0.06	0.1
Trees/ha	0.10	0.09	0.21	-0.08	0.11	-0.12	-0.09	-0.08	0.03	-0.03	-0.03	0.04	0.10
% Canopy Cover	-0.14	-0.06	-0.20	-0.01	-0.03	-0.07	0.02	0.08	0.11	*0.19	0.02	-0.05	**0.29
Plot Basal Area	-0.25	*-0.35	0.26	-0.01	-0.14	0.30	0.26	-0.02	-0.10	0.14	0.17	0.08	*0.25
Elevation	-0.19	*-0.36	0.27	-0.11	-0.01	-0.07	0.25	-0.12	**0.24	0.05	0.25	-0.03	0.00
Heat load	0.15	0.21	-0.13	-0.15	**0.53	-0.05	*0.45	0.11	**0.37	-0.13	0.01	-0.10	**0.31
Time Since Disturbance	*-0.33	0.08	**0.29	-0.05	0.05	-0.15	0.31	**0.30	-0.13	0.08	NA	-0.04	**0.34

Discussion

We found only a modest number of environmental correlates of tree growth and their effects were site-specific. Only two of the five tree species tested had even a single variable with significant correlations at more than two sites, and whenever there were two or more sites with significant correlations for a given variable and species, conflicting relationships occurred more than half the time. It is worth noting that an earlier study using these same sites and plots (Murphy, 2008) showed that environmental variables frequently differed by community type but that the relationships differed by site. Taken together, the findings of these two studies strongly suggest that environmental variables are related to both tree growth and succession in former oak savanna in complex ways that vary from place to place.

Our best regression models were for *Q. garryana* growth, but no model was repeatable across sites. Our best (if still poor) correlations are comparable to a previous study for this species (Gould et al., 2011). This poor predictive power could be due to (i) small sample sizes, (ii) failing to measure the relevant environmental variables or (iii) the complex histories of disturbance and land use at our study sites, which may limit the presence of strong and consistent signals for environmental controls over tree growth. We consider each of these potential explanations in turn.

Our large sample sizes for some species at some sites makes lack of statistical power an unlikely explanation for low predictive power in many cases. This explanation is even more unlikely for all species when cross-site comparisons were made.

We measured a broad suite of edaphic, topographic, and competition-related environmental variables that could potentially control tree growth rates. The fact that nearly all variables were correlated significantly with tree growth for at least some species at some sites suggests that these variables were appropriate. However, other factors may also exert more fundamental controls. For example, water limitation may be an important controlling variable that was not accounted for, and this limitation would be expected to vary by species. Previous research at a small subset of these study plots examined seasonal water availability using moisture wells (Murphy, 2008), and found that soil moisture differed by community type, and that plots with the least water in the soil profile have experienced less forest succession. The same study also found that

community types were strongly associated with site-specific variables such as soil texture and heat load, even though these variables were not strongly correlated with tree growth in this study. The only nutrient we measured was nitrogen. Although other nutrients (e.g., calcium) can be limiting for tree growth in western Oregon forests (Cross and Perakis, 2011), this would be expected only following the dominance of red alder (*Alnus rubra* Bong.), a nitrogen-fixing species (Perakis and Sinkhorn, 2011), which has never been common at our study plots. Individual-based measures of canopy competition and dominance may more accurately capture the influence of competition on tree growth than our plot-wise measurements (Biging and Dobbertin, 1995), although a study using individual-tree measures of competition for *Q. garryana* across a range of sites in the Pacific Northwest found correlations that were comparable to those described in the present study for several of our individual sites (Gould et al., 2011).

We postulate that the weak correlations between tree growth rates and environmental variables in our study are due in large part to the complex histories of disturbance, land-use and management at our study sites. For example, the spatial patterns of land use and management are influenced by the heterogeneous topography and soils of these sites (Wu and Johnson, unpublished data), which complicates assessment of the influence of topography and soils on tree growth. We attempted to control for the differential effects of anthropogenic influences on tree growth rates by estimating time since disturbance, based on reconstruction using historic air-photos. While time since disturbance did correlate significantly with recent tree growth for some species at some sites, time since disturbance may not adequately capture the effects of different types of disturbances on recent tree growth rates for the species in our study. Unlike our study, many dendrochronological studies are designed to limit the effects of interactions among environmental and biological factors (Speer, 2010). Our study suggests that in landscapes with complex relationships between landform, succession, and disturbance, the strong relationships between tree growth and environment so clearly demonstrated in other studies may play out in complex and individualistic ways that differ from place to place. Disturbance history is unquestionably a major determinant of forest stand composition and tree growth rates (Devine and Harrington, 2006). A dendroecological approach that was designed to identify growth release could further

elucidate the influence of disturbance on tree growth rates at our sites. Such future work will require a more nuanced description of disturbance history to successfully determine the effect of disturbance on tree growth rates.

Conclusions

This study enhances our understanding of the growth of the dominant tree species found in former *Q. garryana* savanna in the southern Willamette Valley. Soils, topography and competition all affect the growth rates of these species. The specific effects of different environmental variables on tree growth were not consistent across the landscape, and varied among species as well. The complex disturbance history of these habitats likely contributes to variable dominance of different classes of environmental controls over tree growth rates and the some times opposite effects of the same factor from one site to another. Other habitats that are subjected to mixed disturbance regimes consisting of natural disturbances and human land management will likely show similarly variable spatial patterns of environmental controls over tree species growth, competition, and successional trajectories.

Bridge to Chapter III

In this chapter, we examined the growth rates of dominant tree species in current and former Oregon white oak savanna. We found a significant interaction between the effects of species and site on tree growth rate, a significant main effect of site, but no significant main effect of species. There were site-specific correlations between growth rate and key environmental variables. The complex histories of disturbance and land use created inconsistent relationships between growth rates and environmental variable, which should be considered in conservation and restoration of these ecosystems. In the following chapter, we document the current potential fire behavior in these ecosystems. Further, we explore the degree to which environmental variables and plant community composition can be used to predict potential fire behavior.

CHAPTER III

ECOLOGICAL CORRELATES OF FUEL DYNAMICS AND POTENTIAL FIRE BEHAVIOR IN FORMER UPLAND PRAIRIE AND OAK SAVANNA

A paper published in *Forest Ecology and Management*, co-authored with Scott D. Bridgham, Jane Kertis, and Bart R. Johnson.

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Introduction

Changes in land use following Euro-American settlement across North America have drastically changed vegetation and wildland fire behavior. Many ecosystems that historically experienced low-intensity fires with high frequency now have less frequent, more intense fires (Miller et al., 2009; Schwilk et al., 2009). In the western United States, the most important land use changes include fire exclusion and suppression, timber harvest, grazing and the cessation of Native American burning ((Parsons and DeBenedetti, 1979; Agee, 1996). Land managers now face potential fires that are well outside the range of historic variability in intensity and frequency (Stephens et al., 2009). Where open forest and grassland communities once existed, with grass as the main carrier of fire, there are now dense woodlands and forests.

This rapid succession to novel community types poses unique challenges for land managers, who need to know current fuel loads to assess potential wildland fire behavior and reduce the risk of catastrophic wildland fire. Ground, surface and aerial fuels provide the energy for wildland fires. The way that a particular combination of these fuels burns determines the heat regime of a given fire. Novel plant communities may have different primary carriers of fire – shrubs, leaves, or large branches – that substantially alter fire behavior. Increased stem densities and fuel loads in the forest canopy also allow for new types of fire behavior, such as active crown fires. The ability to predict where and how forest succession may affect fuel loads and fire behavior over time would be useful for assessing the long-term effectiveness of treatments intended to reduce the risk of

catastrophic wildland fire.

Simulation models of fire behavior, such as BehavePlus (Andrews et al., 2008), combine variables that describe the three components of the “fire triangle” – weather, fuels and topography (Countryman, 1972) – using mathematical relationships (Rothermel, 1972; Scott and Reinhardt, 2001) to produce quantitative measures of fire behavior (e.g., heat-per-unit area, crown fire transition ratio). The data to parameterize fire behavior models are precise and quantitative, but data collection is time consuming and expensive. This difficulty has motivated wildland fire managers to develop standardized fuels models (Scott and Burgan, 2005). Land managers from a broad variety of disciplines appreciate simpler models that require fewer data to predict wildland fire behavior (Ager et al., 2007; Lehmkuhl et al., 2007; Fiore et al., 2009), but accurate application of these fuel models still requires detailed data on plant community composition, fuel characteristics, and expected fire behavior (Scott and Burgan, 2005).

Application of fuel models to poorly characterized plant communities requires expertise with both the plant communities and the details of the fuel models themselves. Since fuels derive from vegetation, feedbacks among climate and fire weather, vegetation and fuels, and topography become increasingly important over time scales sufficient for substantial successional and human land use changes (Whitlock et al., 2008). If there are predictable relationships between successional trajectories and fuel loads, we may be able to use successional history to help predict current and future fire behavior.

For this study, we examined how the successional dynamics of extant and former Oregon white oak (*Quercus garryana*, Dougl. ex Hook.) savanna and upland prairie in the southern Willamette Valley, Oregon, USA, have affected fuel loads and potential fire behavior. Oak savanna ecosystems were once widespread throughout North America (Thomas and Spicer, 1987), with over 225,000 hectares in the Willamette Valley (Vesely and Tucker, 2004). Oregon white oak savanna is a fire dependent ecosystem (Habek, 1961) that now occupies substantially less than 10% of its historic area (Hulse et al., 2002). Over the past 150 years, succession has transformed large areas that were oak savanna into woodland or dense forest of mixed species composition. Fire exclusion and suppression by Euro-American settlers have driven this succession (Sprague, 1946; Agee, 1996). Upland prairie, which occupied over 275,000 ha in the Willamette Valley, has

experienced similar losses due to land use changes, including forest succession. Savanna and upland prairie ecosystems support a number of endangered and threatened species (Hosten et al., 2006), and provide valuable ecosystem services, such as the regulation of fire regimes across a landscape. Restoration of these ecosystems, and management that retains these ecosystems over time, may therefore conserve threatened and endangered species and reduce the risk of catastrophic wildfires. These reasons motivate conservation and restoration of oak savanna ecosystems and add value to accurate predictions of fire behavior for extant and former oak savanna communities. We are aware of only one previous study that measured detailed fuel loads in former Pacific Northwest upland prairie and oak savanna, and that study had a total of 21 plots (Ottmar et al., 2004). Because our study provides a novel data set on fuel loads for these forest cover types, we were interested in comparing fire behavior predictions using standard fuel models (Scott and Burgan, 2005) with predictions from our fuels data. Our goals for this study were to: (1) assess the relationship between plant community structure and fuel loads within current and former Oregon white oak savanna communities, (2) assess the relationship between plant community structure and potential fire behavior within these communities, (3) determine the extent to which successional changes have altered potential fire behavior in these communities, and (4) assess how savanna restoration could affect the risk of catastrophic wildland fire.

Materials and Methods

Study Areas

We established over 239 study plots at seven sites in the southern Willamette Valley, Oregon (Figure 3.1). The seven sites were selected to capture the range of environmental variability and current range of successional states found in former savanna ecosystems. We chose these sites based on the range of plant communities present at each site and the cooperation of private and public land managers. To confirm that all plots were located in former upland prairie or Oregon white oak savanna at the time of Euro-American settlement, plot locations were recorded using GPS and entered into a GIS layer in ArcGIS (ESRI 2009). The plot layer was overlain on a map of 1851 vegetation (Pacific Northwest Ecosystem Consortium,

<http://www.fsl.orst.edu/pnwer/wrb/access.html>).

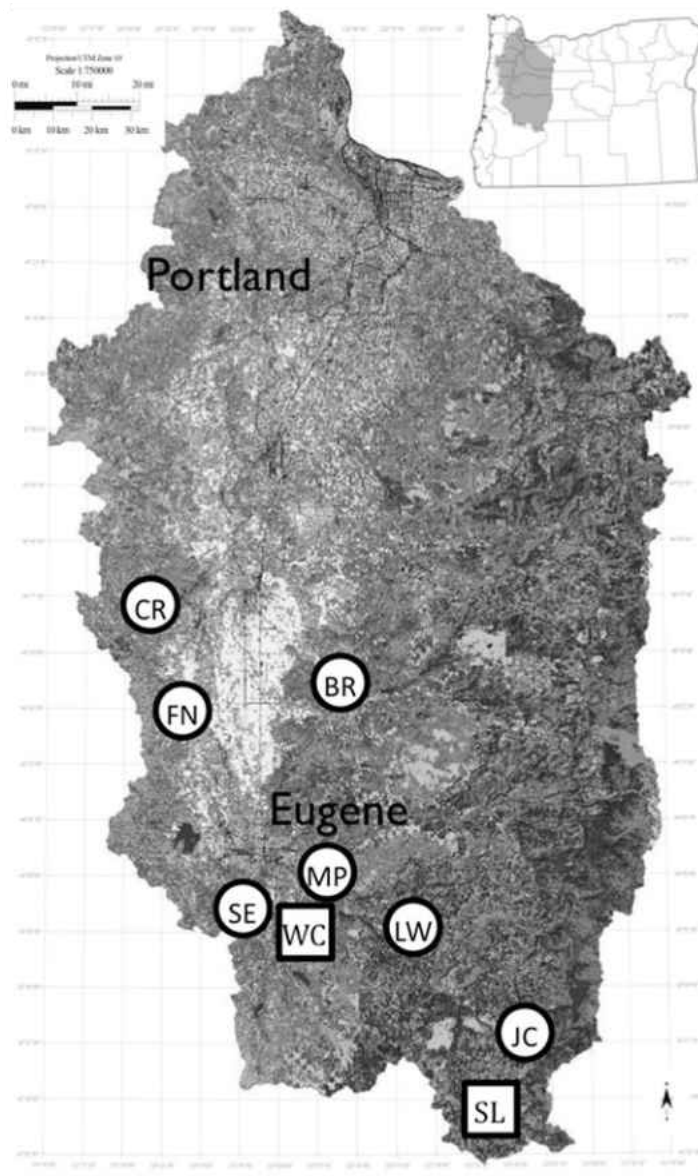


Figure 3.1. Location of the Willamette River Basin within Oregon, USA. White circles indicate study sites in the southern Willamette Valley, with site codes inside. Weather stations are indicated by white squares: WC = Willow Creek, SL = Sugarloaf, Finley RAWS station is at the Finley study site.

There is substantial variation in elevation and soils among and within sites (Table 3.1, Figure 3.1). Sites are either on the valley floor (Finley), on buttes within the valley

(Chip Ross, Mount Pisgah, and South Eugene), or in the foothills of the Cascade Mountains (Lowell, Brownsville, and Jim's Creek). Soils in most sites were predominantly Mollisols and Inceptisols, but three sites also had areas with Ultisols. The dominant tree species are Oregon white oak and Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*, Mirb.). Other prominent tree species include ponderosa pine (*Pinus ponderosa*, Doug. ex Lawson), incense cedar (*Calocedrus decurrens*, Torr. ex Florin), and bigleaf maple (*Acer macrophyllum*, Pursh.).

Environmental Sampling Methods

At each site, we established transects to span important changes in physical and environmental gradients, with the center of a plot placed every 60 m along each transect. Species and diameter at breast-height (DBH) categories (<12, 12-25, > 25-50, > 50-75, > 75-100, > 100 cm) were recorded for every tree within 8 m of plot-center. Supplementary data for large trees were recorded for a 30-m square around plot-center.

We measured all variables at every plot (Table 3.2), excepting soil depth-to-obstruction, which we measured at a subset of plots. We recorded percent slope using a clinometer, averaging an up-slope and a down-slope measurement, and recorded aspect using a compass. We measured tree canopy cover between July and September with a spherical densiometer (Lemmon 1956). We recorded percent cover of the ground layer, shrubs, forbs, graminoids and moss by ocular estimation using the Braun-Blanquet method (1932), with Daubenmire's (1959) modification.

We took random soil samples from 0 to 5 cm depth using a bulb planter (dia. 5.7 cm), and from 5 to 20 cm depth using an Eigelkamp soil auger (dia. 5.0 cm), compositing three soil samples from each depth (Murphy 2008). We also randomly took ten O-horizon samples with a bulb planter from each plot. Soil bulk density was based on the sample volume and dry mass of soil samples dried at 60 °C. We measured soil pH in a 1:1 soil-water slurry. To determine clay content, we used a modified Gee and Bauder (1986) hydrometer method. We isolated sand with a 53- μ m sieve, and then oven-dried and weighed it; percent silt was determined by subtracting the percents of silt and sand from 100. We determined total carbon and nitrogen levels with a Costech Analytical CN analyzer (Murphy, 2008).

Table 3.1

Site name, latitude, longitude and elevation range of the study sites

Site	Site Code	Latitude	Longitude	Elevation Range (m)	Number of plots	Soil Orders
Finley	FN	44°25'N	123°19'W	85 - 165	30	Ultisol, Inceptisol, Mollisol
Chip Ross	CR	44°34'N	123°16'W	183 - 259	29	Mollisol, Inceptisol
Mount Pisgah	MP	44°00'N	122°58'W	171 - 347	24	Mollisol, Inceptisol, Ultisol
South Eugene	SE	44°03'N	123°06'W	201 - 347	25	Mollisol, Inceptisol
Lowell	LW	43°55'N	122°46'W	305 - 488	22	Mollisol, Inceptisol
Brownsville	BR	44°23'N	122°59'W	183 - 610	29	Mollisol, Inceptisol, Ultisol
Jim's Creek	JC	43°30'N	122°25'W	597 - 988	80	Inceptisol

Fuel Sampling Methods

We collected ground, surface and aerial fuels data at 239 plots using Brown's methodology (Brown, 1974; Brown and Roussopoulos, 1974). We placed a 30-m transect perpendicular to the main transect in the center of the plot. Five meters from the center of this new transect we measured the depth of woody and herbaceous fuel beds, litter and duff. We used the following standard categories for fuel diameter to define these fuel time-lag classes: 1-hour fuels < 0.6 cm diameter; 10-hour fuels 0.6 – 2.5 cm diameter; 100-hour fuels > 2.5 – 7.6 cm diameter; 1,000-hour fuels > 7.6 cm diameter (Brown, 1974). We counted each piece of dead, downed woody fuel that intersected the plane of the transect between 6 m and 7 m, and between 23 m and 24 m. To improve the accuracy of large fuel estimates, we counted 1,000-hour fuels along the entire length of the 30-m transect. All ground fuel-load calculations per plot followed Brown (1974).

For aerial fuels, we recorded the number of trees in a plot, DBH class, health status, and crown class for each species. For all trees over 100-cm DBH we recorded individual tree data. Health classes were indexed as healthy, unhealthy, sick and dead, as determined by estimation of limb loss, foliage condition and visible fungal growth (Keen, 1943). Crown classes were dominant, co-dominant, intermediate and suppressed (Smith et al., 1997). We recorded average values for tree height (m), percent live crown, height to live crown, and canopy base height for each species x DBH x health class x crown class group that was present. We recorded tree height using an Impulse LR laser range

Table 3.2

Variables used in this study

Variable	Units
<i>Vegetation, Topographic and Soils Data</i>	
Slope	%
Aspect	degrees
Heat Load	<i>dimensionless</i>
Tree Canopy Cover	%
Moss Cover	%
Ground Cover	%
Graminoid Cover	%
Forb Cover	%
Woody Ground Cover	%
Shrub Cover	%
Basal Area (by species)	%
Small, Medium and Large Trees per Plot by Species	Number of trees
Soil Depth-to-obstruction	cm
Soil Bulk Density	g/cm ³
Soil pH	pH
Soil Sand	%
Soil Silt	%
Soil Clay	%
<i>Fuels Data</i>	
1-hour Fuel Load	Mg/ha
10-hour Fuel Load	Mg/ha
100-hour Fuel Load	Mg/ha
1000-hour Rotten Fuel Load	Mg/ha
1000-hour Sound Fuel Load	Mg/ha
Wood Fuel Bed Depth	m
Herbaceous Fuel Bed Depth	m
Canopy Base Height	m
<i>Calculated Fire Behavior Data</i>	
Heat-per-unit Area	KJ/m ²
Crown Fire Transition Ratio	<i>dimensionless</i>

finder (Laser Technologies Inc.). We defined height to live crown as the height at which branches with living foliage were attached to the trunk. Canopy base height for a plot

was calculated in the field as the lowest height above which there was estimated to be sufficient bulk density to carry fire to the top of the canopy. For each plot we recorded the fuel model that best captured the dominant carrier of fire (Scott and Burgan, 2005).

Forest Cover Types

We defined forest cover types both by canopy structure and tree species dominance. For structure, we measured percent canopy cover of trees, which we classified into the following categories: prairie < 6%, savanna < 25% but \geq 6%, woodland < 60% but \geq 25%, forest \geq 60% (Grossman et al. (1998), with an added division to separate savanna from prairie). It was therefore possible to have trees in a prairie plot. We also subdivided woodland and forest plots based on the ratio of coniferous to deciduous basal area: coniferous \geq 0.67, deciduous \leq 0.33, and $0.33 <$ mixed < 0.67. There were eight forest cover types in our study: prairie (n = 36), savanna (n = 24), deciduous woodland (n = 34), coniferous woodland (n = 10), mixed woodland (n = 17), deciduous forest (n = 11), coniferous forest (n = 77), and mixed forest (n = 16). We excluded fourteen plots from analysis due to missing plant community data.

Fire Behavior Modeling

We analyzed both the field-calculated fuel load variables, and the model-calculated fire behavior variables for surface and crown fire. For fire behavior, we selected heat-per-unit area (HPA) as a surface fire parameter and crown fire transition ratio (CFTR) as a crown fire parameter. HPA, more than rate of spread, flame length, etc., provides an indication of the ecological effects of fire on above- and below-ground vegetation, animals and microbes (Berry, 1970; Van Wagner, 1973; Swezy and Agee, 1991; Acea and Carballas, 1996; Yeager et al., 2005). HPA was calculated following Rothermel (1972), and depends on the surface fuels that affect fire spread. After an extensive search, we could find no canopy fuel data for Oregon white oak, which limited our ability to calculate crown fire behavior parameters. For our analyses, we chose to use the crown fire transition ratio (CFTR). This ratio depends on the fireline intensity of the fire, the foliar moisture content of the aerial fuels, and the canopy base height. The CFTR is calculated as the surface fireline intensity divided by the critical surface

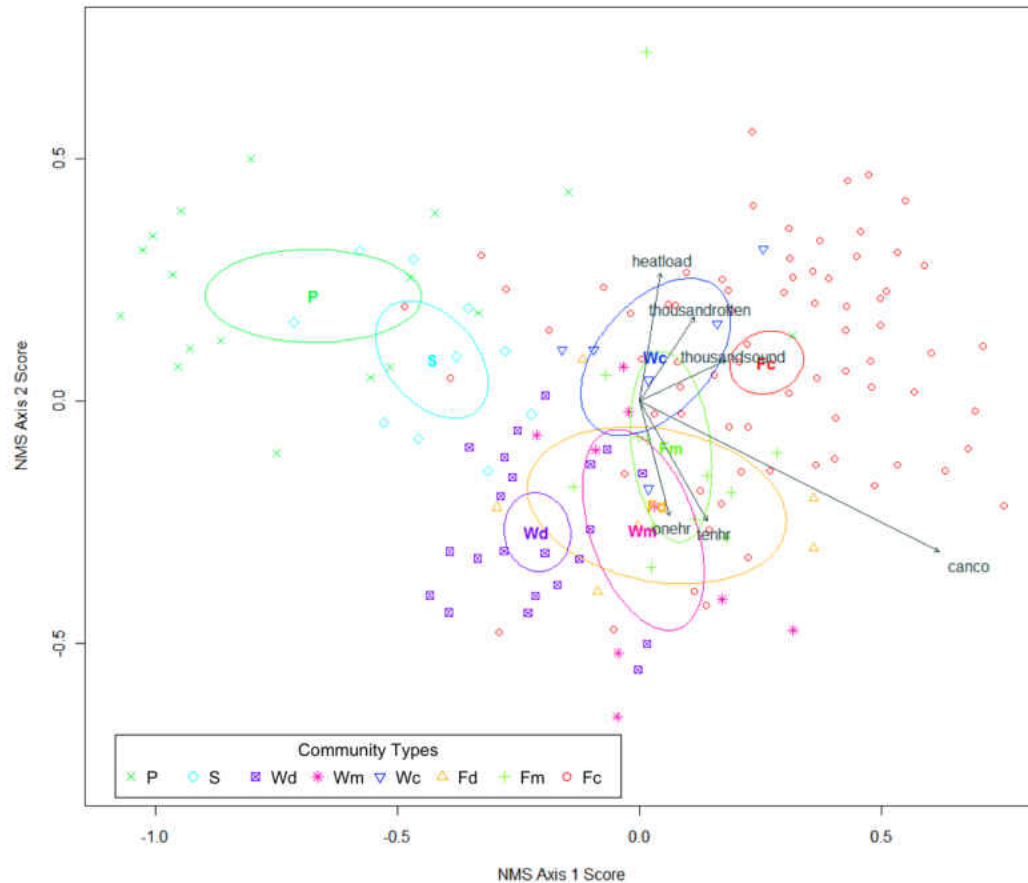


Figure 3.2. Ordination of plots by plant community variables. Ellipses represent 95% confidence intervals of the estimate for the group centroids. Environmental variables that loaded significantly into the ordination space are shown in gray. Environmental variables shown are one-hour fuels (onehr), ten-hour fuels (tenhr), percent canopy cover (canco), thousand-hour sound fuel (thousandsound), thousand-hour rotten fuels (thousandrotten), and heatload. Forest cover types are P = prairie, S = savanna, Wd = deciduous woodland, Wc = coniferous woodland, Wm = mixed woodland, Fd = deciduous forest, Fc = coniferous forest, Fm = mixed forest. We used non-metric multidimensional scaling (NMS) in R, using the package *vegan*, to perform an ordination of our plots. The NMS was based on our plant community data. Variables included percent cover of moss, graminoids, forbs, shrubs, total woody cover, total ground cover, and tree canopy cover, as well as the number of trees for each species in each of three size classes (small, 1-<25 cm DBH; medium, 25-50cm DBH; large, >50cm DBH) (Figure 2).

intensity. When the ratio is greater than or equal to one, the surface fireline intensity is sufficient for a transition to crown fire (Andrews et al., 2008). Because canopy bulk densities are unknown for many of our study species, and because we did not collect those data for this project, we restricted ourselves to only considering CFTR, which does not rely on estimates of canopy bulk density.

We used BehavePlus (Andrews et al., 2008) to calculate HPA and CFTR. BehavePlus uses Rothermel's model of fire spread (1972), which treats fire spread as series of individual ignitions. BehavePlus requires fuel characteristics, topographic characteristics and fire weather variables to model HPA and CFTR (Andrews et al., 2008). We used field-based estimates of canopy base height, and created custom fuel models by using our field-based surface fuel loads for each plot. We used percent slope and FireFamilyPlus 4.0 to calculate 90th and 97th percentile fire weather data (wind speed and fuel moisture), based on historic data from local weather stations. We used data from three weather stations to represent our sites: Willow Creek (NESS ID 324A320E) for SE, MP and LW, Finley National Wildlife Refuge (NESS ID 837507E2) for CR, BR and FN, and Sugarloaf (NESS ID 323653D8) for JC (all data available at <http://www.ncdc.noaa.gov/oa/climate/stationlocator.html>). BehavePlus has been used successfully in a wide variety of environments, although it tends to perform worse in areas with highly structured fuels (Glitzenstein et al., 2006).

Fire behavior parameters always differed significantly and consistently between 90th and 97th percentile fire weather simulations. For heat-per-unit area, 90th and 97th percentile weather values were highly correlated ($r = 0.999$), and 97th percentile values were consistently higher than 90th percentile values ($p < 0.001$). This is due entirely to the mathematical equations that drive BehavePlus. For these reasons, we used fire behavior parameters from 97th percentile fire weather as dependent variables in our analyses.(Ottmar et al., 2004)(Scott and Burgan, 2005)

Statistical Analyses

There was no relationship between a plot's standard fuel model-based prediction of HPA and its custom fuel model-based prediction of HPA ($r^2 < 0.001$), indicating that standard fuel models do not adequately summarize fuel loads or potential fire behavior

for our study area. Consequently, we analyzed our plot data using two different approaches based upon custom fuel models. First, we checked for differences in fuel and fire behavior variables among forest cover types using the nonparametric Kruskal-Wallis rank sum test (Kruskal and Wallis, 1952). We used a nonparametric test because our data were non-normally distributed, with highly unequal variances and sample sizes among forest cover types. We made pair-wise comparisons between forest cover types using Wilcoxon's rank sum test (Wilcoxon, 1945), with Benjamini and Hochberg's (1995) correction to control for Type I error. Second, we used Classification and Regression Trees (CARTs) in R (R Development Core Team, 2008), using the *rpart* package v.3.1-45 (Therneau and Atkinson, 2010) to differentiate groups of plots in terms of fire behavior. CARTs determine groups for a dependent variable by binary splitting of categorical and continuous independent variables (Breiman et al., 1984). The algorithm that grows the CART selects independent variables in decreasing order of how much variance they explain in the dependent variable. We generated separate CART models to predict surface fire and crown fire behaviors. Both models were offered the entire suite of vegetation, topographic, and soils data collected from our seven study sites (Table 2) as independent variables. These included the same plant functional type covers and tree species data used in the NMS ordination, as well as total basal area by tree species. We chose not to use fuel load parameters (e.g., Mg of 1-hour fuels/ha) as independent variables in the CARTs for three reasons. First, using these factors as independent variables to predict the outputs of BehavePlus would essentially constitute a sensitivity analysis of the model, something others (Brose and Wade, 2002) have already undertaken. Indeed, analyzing our data in this way indicates that 1-hour fuels are overwhelmingly important for predicting HPA ($r^2=0.59$). Second, it may not be possible for land managers to adequately collect these data. Third, a major goal of this study is to predict fire behavior based on plant community structure and successional history. Knowing that 1-hour fuels strongly influence how BehavePlus calculates potential fire behavior does not provide insight into the relationships between successional dynamics and fire behavior in former prairie and savanna plots that we wished to investigate.

After using a CART to identify groups of plots on the basis of surface fire behavior, we ran CARTs on two of the subgroups established by the original CART to

further explore the distributions, dynamics and variance among plots in the study. To perform a CART on crown fire behavior, we divided the CFTR into eight categories (Table 3.3) because of the extreme positive skew of the variable. While CART analysis is a nonparametric technique that does not inherently require normal data distributions, CFTRs near 1 are most important because this is the point at which a fire may enter the canopy. Our categories allowed us to emphasize values near 1.

Results and Discussion

Forest Cover Types

Ordination of the plots by NMS was able to differentiate prairie and savanna from the wooded community types (Figure 3.2). The ordination was less successful at differentiating wooded community types from each other. The total stress for the model was 19.65 on two axes. The first axis had strong negative loadings for graminoid cover, total ground cover, and large Oregon white oaks, and strong positive loadings for medium and large incense cedars, and large ponderosa pines. The second axis had strong negative loadings for small and medium bigleaf maples and strong positive loadings for small and medium incense cedars, and large ponderosa pines. The ordination revealed a gradient from deciduous through mixed to coniferous that was consistent for woodland and forest, even though it did not show these groups to be significantly different. Two environmental variables loaded significantly into this ordination space: percent canopy cover ($p=0.001$) and heatload ($p=0.005$). The trends from deciduous to coniferous wooded types, as well as the significant loading of canopy cover into the ordination space, provided validation for the eight forest cover types.

Table 3.3

Ranges of crown fire transition ratio values in the categories used for CART analysis

Transition Ratio	0 < 0.01	< 0.05	< 0.5	< 1.1	< 2	< 10	< 100	< ∞
Group ID								
(in Figure 8)	a	b	c	d	e	f	g	h
Sample Size	68	28	60	18	15	22	25	3

Variation in Fuel Loads by Forest Cover Type

Four fuel variables had significant loadings into the ordination space (Figure 2). These were ten-hour fuels ($p < 0.001$), one-hour fuels ($p = 0.007$), and both rotten ($p = 0.03$) and sound ($p = 0.04$) thousand-hour fuels. While all fuel characteristics differed significantly by forest cover type, there was no consistent monotonic trend for all fuel size categories across forest cover types, excepting that prairie and savanna usually had significantly lower fuel loads than woodland or forest plots (Figures 3 and 4). Furthermore, fuel loads were lower in prairie than in savanna for 1-hour (Figure 3A) and 10-hour fuels (Figure 3B). For each fuel time-lag class, there was usually some forest type that had a significantly higher fuel load than some woodland type, but these relationships were not consistent across fuel time-lag classes.

Fuel-bed depths differed significantly among communities for both herbaceous and woody fuels. The only pair-wise difference for depth of herbaceous fuels was a marginal one between prairie and mixed woodland ($p = 0.068$, Figure 3.4A). Woody fuel depth in prairie was significantly lower than all other forest cover types (Figure 3.4B). Savanna had the second-lowest woody fuel depth, but was only marginally lower than coniferous woodland ($p = .065$). The woodland and forest types did not significantly differ. The only pair-wise difference in canopy base height was between savanna and coniferous forest ($p = 0.016$).

It is notable that there were no significant pair-wise differences in herbaceous fuel bed depth (Figure 3.4A), even between prairie/savanna and forested plots. Prairie plots and coniferous and deciduous forest plots actually had similarly high median herbaceous fuel bed depths, of approximately 0.3 m.

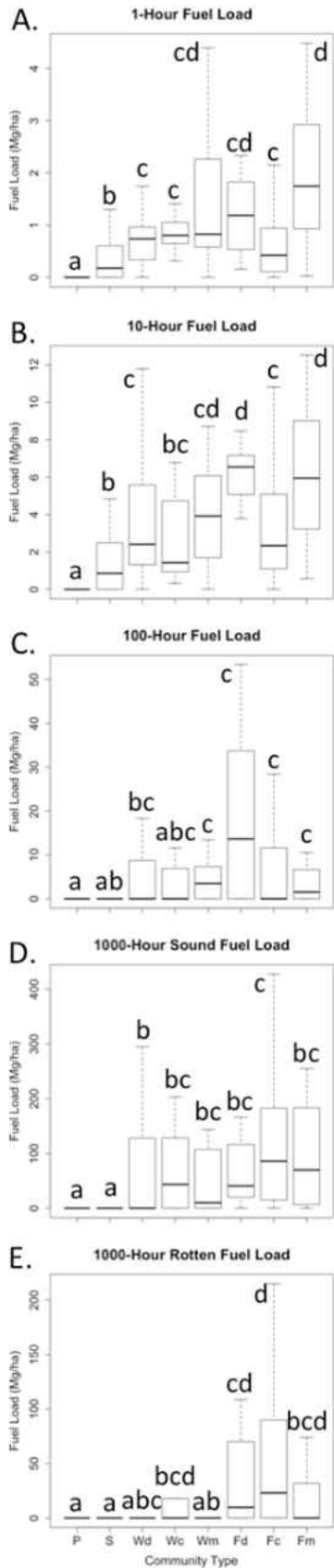


Figure 3.3. Plots of fuel loads by forest cover type. Fuels are represented in fuel moisture time-lag classes: 1-hour (3.3A), 10-hour (3.3B), 100-hour (3.3C), 1,000-hour sound (3.3D), and 1,000-hour rotten (3.3E). Bars indicate the group medians, boxes are drawn between the quartiles, and fences indicate maximum and minimum values, excluding outliers. Lowercase letters above bars indicates significantly different groups, $p < 0.05$. Forest cover types are P = prairie, S = savanna, Wd = deciduous woodland, Wc = coniferous woodland, Wm = mixed woodland, Fd = deciduous forest, Fc = coniferous forest, Fm = mixed forest.

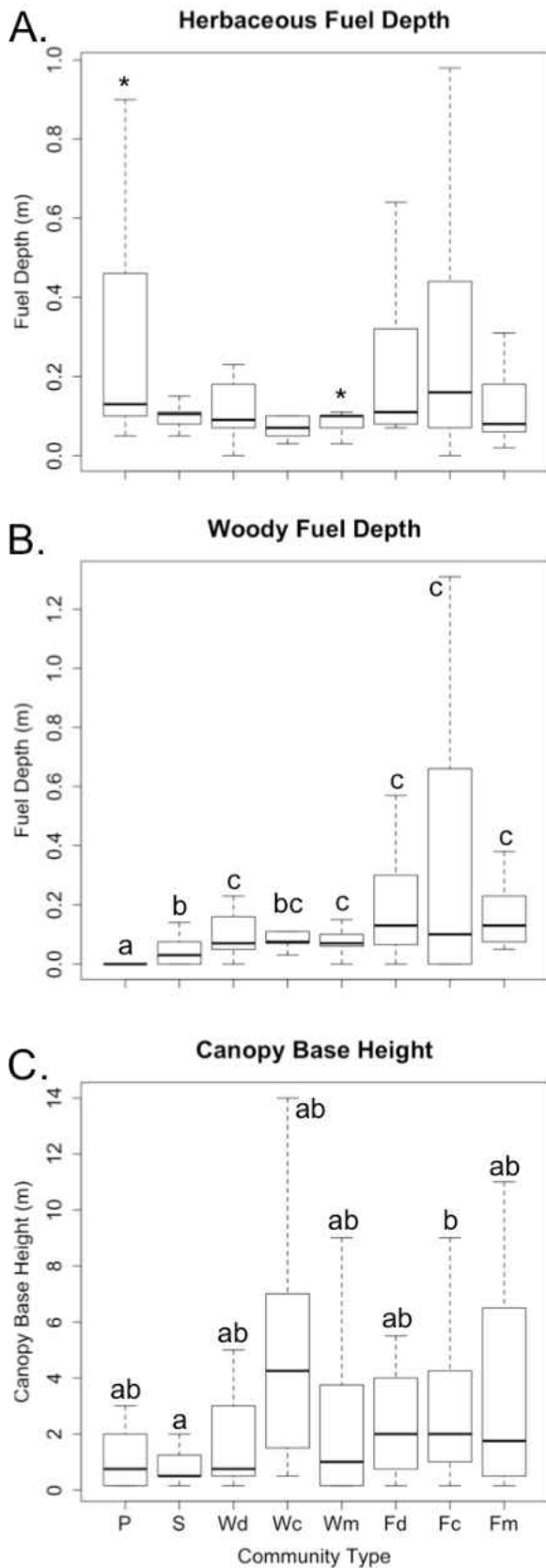


Figure 3.4. Plots of fuel structure by forest cover type. Fuel structural variables are herbaceous fuel depth (3.4A), woody fuel depth (3.4B) and canopy base height (3.4C). Bars indicate the group medians, boxes are drawn between the quartiles, and fences indicate maximum and minimum values, excluding outliers. Lowercase letters above bars indicates significantly different groups, $p < 0.05$. Asterisks above bars indicate groups that are marginally significantly different ($p < 0.10$). Forest cover types are P = prairie, S = savanna, Wd = deciduous woodland, Wc = coniferous woodland, Wm = mixed woodland, Fd = deciduous forest, Fc = coniferous forest, Fm = mixed forest.

The lack of significant differences among forest cover types in the base height of their canopies (Figure 3.4C) is most likely a result of the successional histories of our study plots and the characteristics of oak growth habits. In savanna plots, open-grown trees had low, spreading branches, which often reach to within 0.1 m of the ground. This gave our savanna plots the lowest median canopy base height. But woodland and forest plots shared a similar successional state within the past 150 years, and often more recently than that. Despite their greater tree canopy cover, forest and woodland plots often included oaks that retained low, spreading branches from their successional past. Additionally, these plots were not even-aged stands, often including a mixture of young and old coniferous trees. Coniferous trees often grow below, through, and above the remnant – and quickly senescing – oak savanna canopy. Such mixed-age stands have high tree canopy cover with continuous ladder fuels from a low height to the top of the canopy.

Variation in Fire Behavior by Forest Cover Type

Fire behavior variables did not load significantly into the ordination space (Figure 3.2). The usefulness of the forest cover types in predicting fire behavior was marginal (Figure 3.5). While prairie and savanna formed unique groups with low HPA (Figure 3.5A), the only significant differences for the remaining communities were between mixed forest and coniferous woodland ($p = 0.018$), and mixed forest and mixed woodland ($p = 0.017$). The results for the crown fire transition ratio (CFTR) (Figure 3.5B) were even less straightforward. Prairie had the lowest transition ratio, but the only significant differences for the remaining forest cover types were a higher ratio in deciduous woodland than in savanna, coniferous woodland and coniferous forest. Post hoc power analyses indicate that sample sizes were sufficient to detect significant differences, had they existed. The high and uneven variability of fire behavior by forest cover type contributes to the lack of significant differences in group means (Figure 3.5). Forest cover types with high median HPA or CFTRs also had high variability. Much of the variability comes from a few plots within a forest cover type having extremely high probabilities of transition to a crown fire, as seen in the positive skew of the distribution

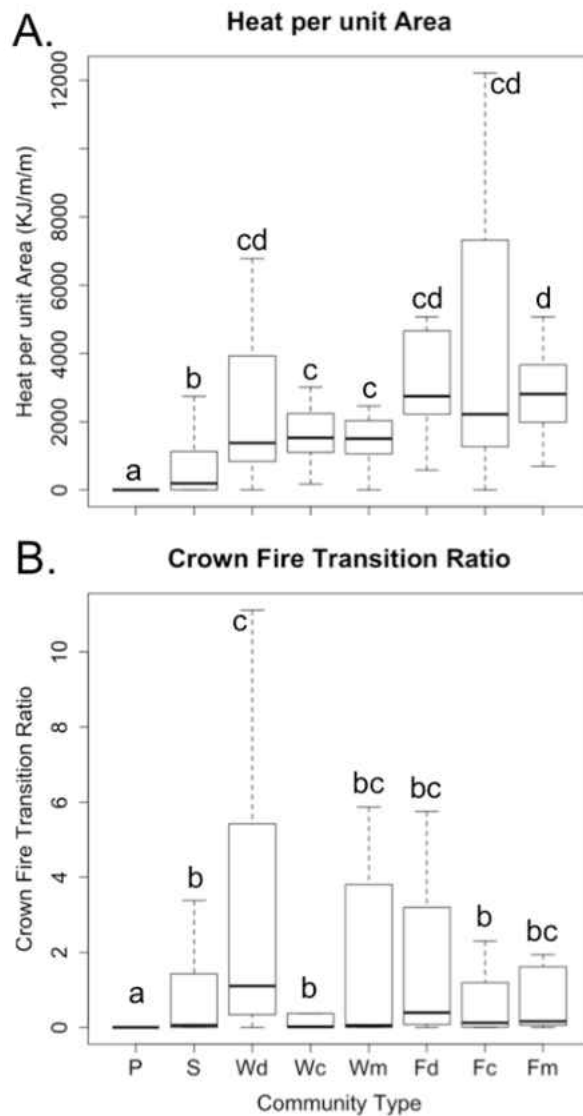


Figure 3.5. Plots of heat-per-unit area (3.5A) and crown fire transition ratio (3.5B) by forest cover type. Bars indicate the group medians, boxes are drawn between the quartiles, and fences indicate maximum and minimum values, excluding outliers. Lowercase letters above bars indicates significantly different groups, $p < 0.05$. Forest cover types are P = prairie, S = savanna, Wd = deciduous woodland, Wc = coniferous woodland, Wm = mixed woodland, Fd = deciduous forest, Fc = coniferous forest, Fm = mixed forest.

of CFTR for nearly all of the forest cover type (Figure 3.5B). To a lesser extent, this is also true of HPA (Figure 3.5A). Situations like these make our forest cover types poor predictors of fire behavior, with the exception of prairie and savanna.

Fire Behavior Community Types – Surface Fire Intensity

For the most part, we could not construct classification and regression trees (CARTs) predicting individual fuel variables from plant community and physical variables. A CART for 1-hour fuels was informative, $r^2 = 0.54$ after pruning, but for all other fuel variables the pruning routine prevented the algorithm from building any model whatsoever. While it would be beneficial to use environmental and physical variables to predict fuels variables, our data indicate that it is not possible to do so for the former Willamette Valley prairie and savanna habitats that comprise our study plots.

Given the limited utility of forest cover types and the NMS for predicting potential fire behavior, we decided to use CARTs to explore underlying ecological predictors of these phenomena. The results of CARTs are substantially different from the results of techniques like multiple regression with model selection by Akaike's Information Criterion. CARTs can indicate non-linearities, and repeatedly include variables that are especially important.

CARTs indicated that topographic and ecological community data, but never soils data, could partially explain surface fire behavior, although the predictive power was modest. Analysis of HPA indicated five terminal groups ($r^2_{\text{adj}} = 0.21$, $n = 228$, Figure 3.6). BehavePlus calculates HPA based on the surface fuels that affect a fire's surface rate of spread. The first split in the CART is at 57% percent tree canopy cover, which is very close to our threshold between woodland and forest. The first variable selected to parse the "forested" plots was heat

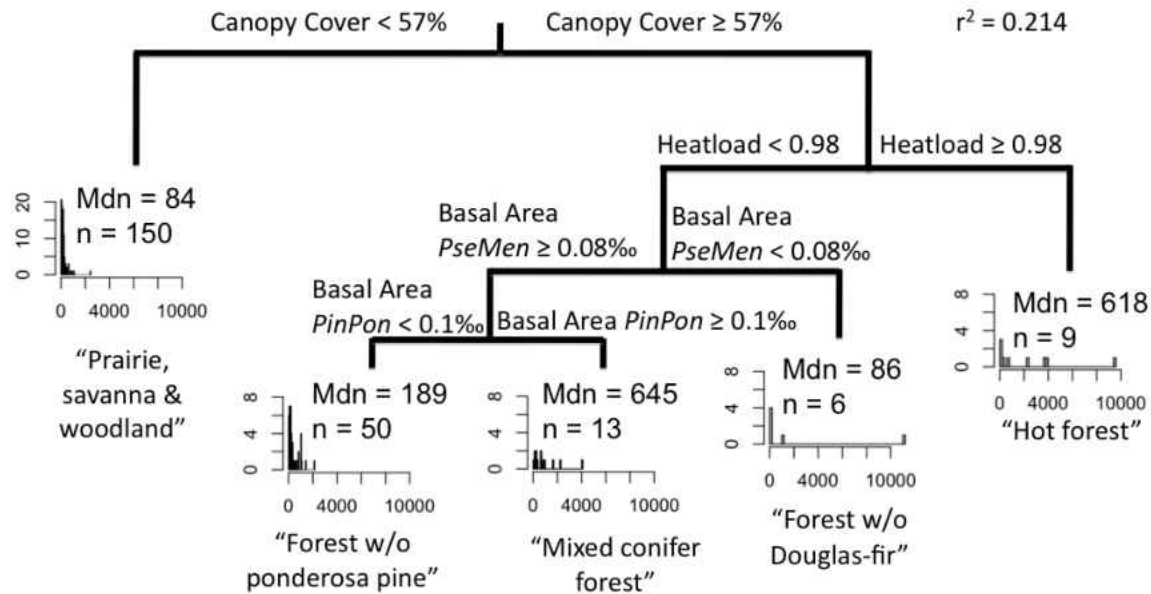


Figure 3.6. CART analysis of heat-per-unit area. Explanatory variables are percent tree canopy cover, heat load, basal area of Douglas-fir (PseMen), and basal area of ponderosa pine (PinPon). For each terminal group we show the group median (Mdn), sample size (n), and a histogram of heat-per-unit area. Although we only report the group median, groups are arranged from left to right in order of increasing group mean. The vertical depth of each split is proportional to the variance explained.

load, with greatest HPA in forested plots with heat load ≥ 0.98 ("hot forests"). Heat load is a dimensionless parameter and is a function of latitude, slope and aspect (McCune and Keon, 2002). For example, at 40° N, a 30° slope with a north aspect will have a heat load of 0.64, while the same slope with a southern aspect would have a heat load of 0.98. Slope, aspect and elevation affect vegetation and therefore fuels, but BehavePlus also uses them directly. There were only nine plots with such high heat loads in our study area – all with steep, southern aspects and dense forest. While this group had the highest mean HPA, the variance was also quite high, indicating low predictability.

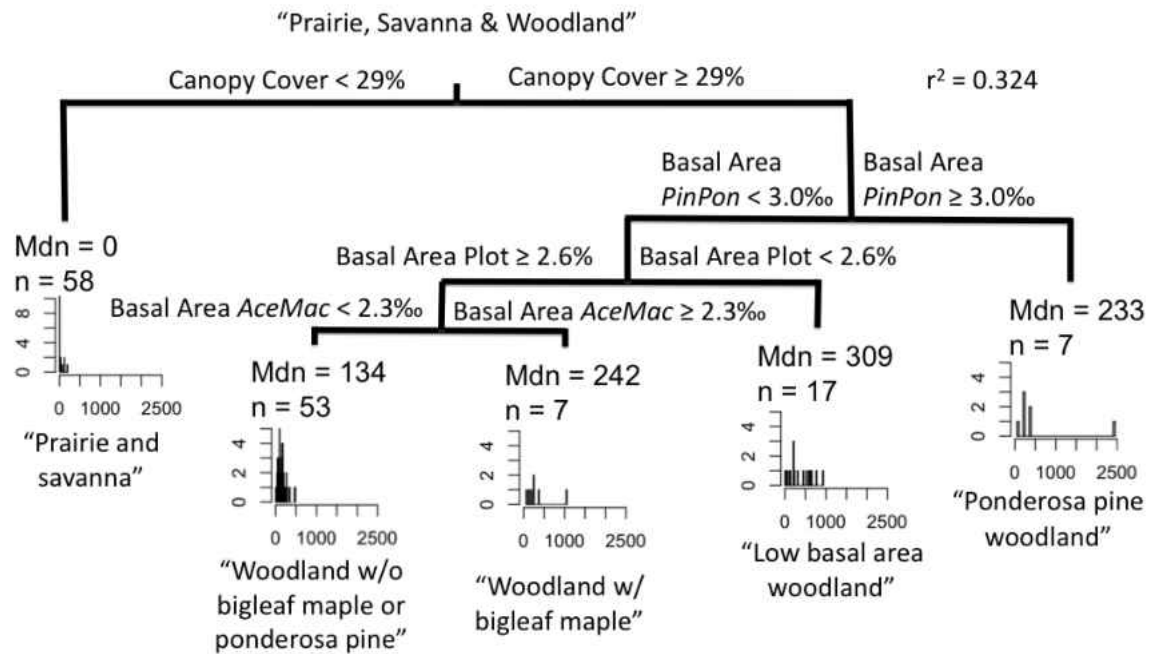


Figure 3.7. CART analysis of heat-per-unit area for "Prairie, savanna and woodland" from Figure 3.6, above. Explanatory variables are percent tree canopy cover, basal area of ponderosa pine (PinPon), basal area of the entire study plot, and basal area of bigleaf maple (AceMac). For each terminal group we show the group median, sample size, and a histogram of heat-per-unit area. Although we only report the group median, groups are arranged from left to right in order of increasing group mean. The vertical depth of each split is proportional to the variance explained.

For plots that have a lower heat load, the next division occurred at extremely low basal area of Douglas-fir ("forests without Douglas-fir"), essentially a binary absence/presence indicator for Douglas-fir. Six forested plots that do not have a high heat load, nor any Douglas-fir, fell into this group. These plots are almost exclusively on one hillside at FN, where there was bigleaf maple forest with a dense and tall understory of shrubs. The final split in the forested plots occurred at low basal area of ponderosa

pine, again an absence/presence indicator. Forested plots with lower heat load and some Douglas-fir, then, are split into two groups: “mixed forest”, with some ponderosa pine, has moderate HPA values; “forests without ponderosa pine” has relatively low HPA values. It is possible that the ponderosa pines themselves may be driving this dynamic – the quantity and distribution of needles and twigs from the pines might significantly increase the HPA within a plot. In this way, the successional history of a stand that was once pine savanna may continue to affect its fire behavior for at least 150 years. Overall, heat per unit area increased by almost an order of magnitude from the “prairie, savanna and woodland” plots, the group with the lowest HPA, to “hot forests,” the group with the highest HPA in this CART.

Because there was a high degree of variability in HPA within terminal nodes for the CART, with greater variance in groups with higher HPA, we reran CARTs on subgroups identified in the original CART to help further tease out variance in the system. A CART re-run on the right side of the original CART yielded no further splits after pruning and even lower predictive power, $r^2_{\text{adj}} = 0.141$, $n = 85$. The initial surface fire CART left 150 plots in the “prairie, savanna and woodland” group. A CART run just on the “prairie, savanna and woodland” group had five terminal groups ($r^2_{\text{adj}} = 0.32$, $n = 144$, Figure 3.6). This added proportion of explained variance is an improvement over the original surface fire CART. Importantly, these two CARTs indicate that we can predict fire behavior with greater precision for fires with less HPA than for fires with more HPA, although the predictive power of even our best model is still modest.

The first split in “Prairie, savanna and woodland” CART occurred at 29% tree canopy cover, close to the threshold between savanna and woodland plots. “Prairie and savanna” had the lowest mean HPA. Species composition distinguishes the other four subgroups. “Ponderosa pine woodland” has at least a small amount of ponderosa pine. Increasing basal area of ponderosa pine consistently corresponds to an increase in HPA in both CARTs. “Low basal area woodland” has tree stems occupying less than 2.6% of its ground area. The amount of bigleaf maple distinguishes “woodland with bigleaf maple” from “woodland without bigleaf maple or ponderosa pine”. Once again, heat per unit area increased by nearly an order of magnitude from the coolest group to the hottest group in this CART.

We also ran a CART on the “prairie and savanna” group from the second surface fire CART; it used only percent tree canopy cover as an explanatory variable. The split at 18% tree canopy cover yielded two terminal groups, with $r^2_{\text{adj}} = 0.514$, $n = 58$. This increase in explanatory power further suggests that the precision of fire behavior predictions increases with decreasing fire intensity and tree canopy cover. This fits well with the results from our pair-wise comparisons, which indicate that prairie and savanna are often different from woodland and forest, and that prairie and savanna are occasionally different from each other.

Taken together, the CARTs for surface fires indicate that community structure is the most important factor driving surface fire behavior in woodland and forest plots, though still describing a minority of the variance. Tree canopy cover, the primary structural feature distinguishing forest cover types, is the most important variable. In particular, BehavePlus predicted surface fire intensity to be consistently low in prairie and savanna. Tree canopy cover thresholds near 57% and 29% distinguish groups of plots with HPA that differ by orders of magnitude. The topography of a plot also appears to be an important control, as shown by heat load. Tree species composition is also quite important, as the particular species in a stand of trees will contribute differently to the fuel load on the ground.

Fire Behavior Community Types – Crown Fire Initiation

We used CARTs to examine CFTR categories (Table 3). The CART produced five terminal groups, with only modest predictive power, $r^2_{\text{adj}} = 0.25$, $n = 237$ (Figure 3.8). BehavePlus calculates the CFTR from the fireline intensity, canopy base height, and canopy foliar moisture content. The first split occurred at 16% tree canopy cover, below the 25% tree canopy cover boundary between savanna and woodland. Most plots in the “prairie and sparse savanna” group had a CFTR below 0.01, with the highest ratio less than 0.5. Thus, plots with less than 16% canopy cover are extremely unlikely to spread a fire from the ground into a tree's canopy. “Low grass” plots generally had lower transition ratios. While most plots in the “woodland and forest - low grass cover” group had a transition ratio less than 0.5, some plots in this group contained a great deal of variability, including two of the three plots most likely transition to a crown fire. The

next split was at 44% tree canopy cover, with “grassy forest and closed woodland” having higher tree canopy cover: once plots were above 16% tree canopy cover, higher tree canopy cover did not increase the probability of transitioning to a crown fire. Finally, percent woody cover differentiated “grass-shrub open woodlands” from

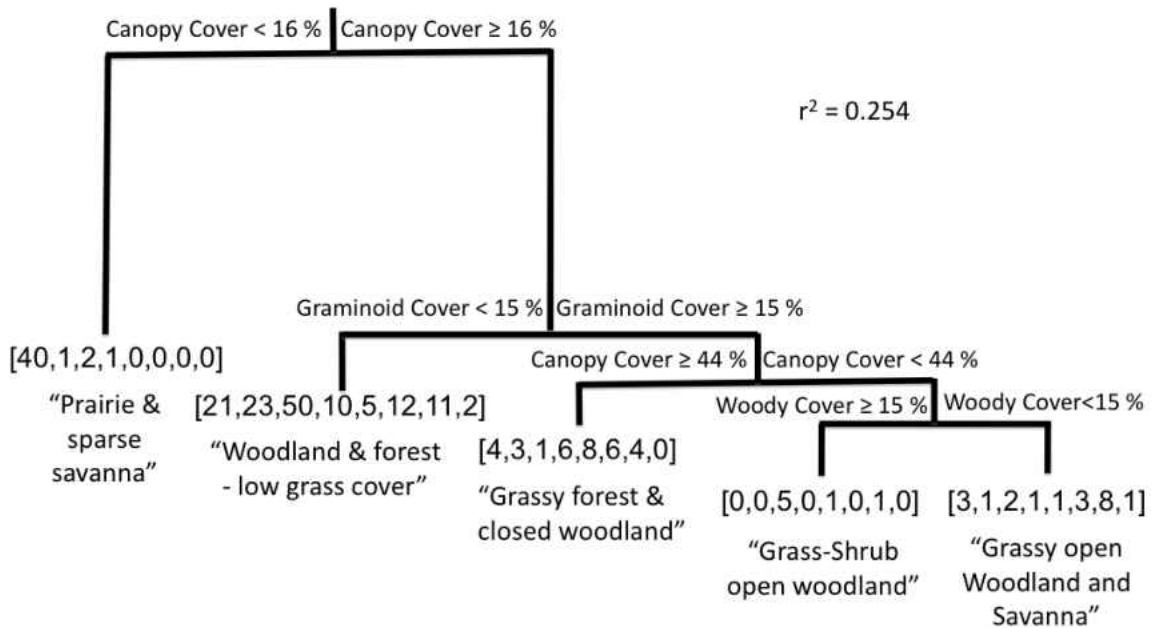


Figure 3.8. CART analysis of crown fire transition ratio. Woody cover refers to woody ground cover only. For each terminal group we show the number of plots in the eight crown fire transition ratio categories as shown in Table 3.3 (with the same order from right to left), from least to most likely to transition to a crown fire. The vertical depth of each split is proportional to the variance explained.

“grassy open woodlands and savanna”, with “grassy open woodland and savanna” having a greater probability of transition to crown fire. It would seem reasonable to assume that increasing woody ground cover and tree canopy cover would increase the likelihood of transition to a crown fire, as ground and canopy fuels would be more

abundant and fire could more easily spread between them. The crown fire CART indicates that the relationship is not so simple in the field. This may be because increasing tree canopy cover leads to self-pruning of the trees, preventing senescent branches from acting as ladder fuels and thereby increasing canopy base height. Although increasing graminoid cover only occurs once in the CART, lower woody ground cover likely corresponds to greater herbaceous ground cover. BehavePlus would translate increased herbaceous ground cover into greater surface fire flame lengths, leading to higher crown fire transition ratios.

The use of CARTs improved discrimination of fire behavior in woodland and forest plots. Our predictive power remained modest in general, although it was good for plots with tree canopy cover less than 16%. While tree canopy cover appeared to be an important community characteristic for fire behavior in general, the CARTs indicated that different types of variables were important in predicting surface and crown fires. Community structure, topography and tree species abundances appeared to be important for surface fires, while only community structure variables appeared to be important for predicting the transition from ground to crown fires.

Conclusions

Our results indicate that commonly accepted descriptions of plant communities provide limited ability to predict fuel loads and fire behavior in a landscape that is in various states of successional transition from oak savanna and prairie to closed-canopy forest. While the standard fuel model approach (Scott and Burgan 2005) is appropriate in many ecosystems, in the habitats that we studied, standard fuel models were not useful for estimating fuel loads (except for 1-hour fuels) and simulating fire behavior. Our data provide a strong basis for the development of new fuel models for these ecosystems. Our study provides some of the most detailed fuels data from lowland habitats in the Pacific Northwest. The legacy of prairie and savanna vegetation appears to have created greater variability in fuels and fire behavior than would otherwise exist in these habitats. In particular, oaks with senescing branches and Douglas-fir growing up through the oak canopy, have led to structural complexity in surface and aerial fuels. It is not surprising, then, that no standard classification method – neither forest cover types nor fuel models –

effectively captures the range of potential fire behavior in these habitats. Our work, however, should encourage land managers working in ecosystems that have undergone similarly complex successional changes to use an analysis similar to the one in this paper to identify critical thresholds and targets for managing wildland fire behavior.

The fuel loads in our plots reflect their current vegetation, but each plot's individual successional history has strongly influenced its current vegetation. For example, plots that had ponderosa pine prior to Euro-American settlement yield forests with distinct fuel loads and fire behavior (see Figure 3.6, "forests without ponderosa pine" versus "mixed forest", and Figure 7, "ponderosa pine woodland" versus the other "woodland" types). This is likely due to the high loads of fine (1-hour) fuels that ponderosa pines generate beneath their canopies. While management may aim to retain these pines for reasons of species diversity, structural heterogeneity, or historical legacy, our study indicates that such management will require extra attention to attenuating fuel loads and fire behavior. Differences in land-use history contribute strongly to fuel loads and fire behavior, so understanding the natural history of an area is crucial to effectively predicting and managing fuels and fire behavior.

Although our data come from small study plots, they offer insights into fire behavior at larger scales that may be useful to land managers. By using CARTs, we have been able to explore our extensive data set and suggest ways to predict and manage fire behavior more effectively than by basing them on conventional forest cover types used for community classification (e.g., broadleaf forest). This is especially true of woodland and forest stands, which are difficult to distinguish in terms of their fuel loads and fire behavior. For example, trying to generally change mixed forest to deciduous woodland, despite the changes in stem density, canopy cover, and species composition, may only marginally affect fire behavior.

The CARTs for surface fire initially followed our structural cover types with cutoffs between combined prairie and savanna, woodland, and forest types, and with increasing HPA from more open to more closed stands. However, it then created splits within the forest and woodland groups that were different than the classifications based on deciduous versus coniferous dominance, principally using the basal area of different tree species to create the groups. Interestingly, the CARTS never used the basal area of

our primary species of interest, *Quercus garryana* in any of the splits. It is notable that the CARTs for both surface and crown fires created nearly identical splits within the prairie/savanna complex (18% and 16%, respectively). In this way, our data identify salient canopy cover thresholds when assessing fire behavior.

Our data suggest which forest and woodland stands might benefit the most from fuels reduction treatments. For most stands, management for fire hazard could focus on the few most important explanatory variables from the CARTs. These include structural variables – percent tree canopy cover, and graminoid and woody ground cover – as well as topographic variables, and the abundances of key tree species. Previous work has also indicated the importance of topography in controlling fire severity (Alexander et al., 2006). For plots where topography strongly controls fire severity, fuels management may need to be more aggressive to achieve a desired outcome. Steep slopes with southern aspects might unacceptably attenuate the benefits of conventional fuel reduction treatments and deserve special consideration from fire managers. Most conventional fuels management relies on treating fuels at regular intervals. Given that no active fuels management has occurred on our sites for several decades, our results may be particularly useful for identifying stand characteristics that reduce fire hazard, even when frequent fuels treatments are unlikely.

Experimental studies of fuel reduction treatments have indicated the primacy of reducing canopy cover and ground layer cover to attenuate fire behavior (Fernandes and Botelho, 2003; Stephens and Moghaddas, 2005; Stephens et al., 2009), although few studies have provided data on individual species abundances similar to our data. By reducing tree canopy cover below 57%, for example, our data indicate that it may be possible to reduce surface fire heat per unit area by nearly an order of magnitude. Key tree species that appear to affect fire behavior in current and former Oregon white oak savanna include Douglas-fir, ponderosa pine and bigleaf maple. For example, the presence of ponderosa pine in plots with more than 29% canopy cover correlates with a substantial increase in surface fire intensity. If managers wish to retain ponderosa pine, they may need to prioritize fuel reduction treatments in stands of this type.

Further, it is clear that surface fire HPA and CFTR are sensitive to different plant community variables. Our CARTs indicate that woodland and forest stands with high

graminoid cover have the highest likelihood of fire moving from the surface to the tree canopy. Lower canopy cover and high woody ground cover in forest and woodland stands, however, may reduce the chances of fire moving from the surface to the tree canopy. The highest CFTR is in stands with intermediate canopy cover, high graminoid cover, and low woody ground cover – these stands should be prioritized for management. This finding reinforces the practice of treating these two types of fire separately to successfully treat the full spectrum of fire behavior. Fuels data and plant community data together will always yield the best predictions of potential fire behavior. Where fuels data are not available, however, our work indicates that it is still possible to make nuanced predictions of fire behavior without relying on standard fuel models. The type of CART analysis that we performed could be useful in other regions, both to identify useful fuels management strategies and to identify types of stands that managers should prioritize.

Our results may also motivate land managers to conserve remnant oak savanna, restore land to savanna or prairie structure, and dedicate resources to eradicating exotic invasive grasses, purely on the basis on ameliorating local fire regimes. While some woodlands and forests have potential fire behavior with low HPA and low CFTR, simulated fires in prairie and savanna have consistently low HPA and CFTR. This may present less risk to life and property. Land managers can meet the challenges of attenuating fire behavior and conserving biodiversity simultaneously by restoring forests and woodlands to prairies and savannas, which may reduce fire intensity by an order of magnitude or more. Creating fire regimes that are more predictable, with lower HPA, lower CFTR, and lower potential for active crown fire to flow across a landscape will be beneficial for both the people and biodiversity that depend on these ecosystems.

Bridge to Chapter IV

In this chapter, we documented fuel loads in current and former Oregon white oak savanna. We simulated potential fire behavior, and looked for relationships between current vegetation, environmental variables, fuel loads, and potential fire behavior. In the following chapter, we use information from Chapters II and III, as well as many other sources, to build, parameterize and test a new climate-sensitive vegetation model. We call this new model CV-STM (Climate-sensitive Vegetation State and Transition Model). CV-

STM is capable of simulating species-level changes in plant communities under changing climate, and can do so in conjunction with mechanistic models of fire ignition, spread, and effects, and mechanistic models of human land-use decisions.

CHAPTER IV

A NEW MODELING APPROACH FOR PROJECTING CLIMATE CHANGE IMPACTS ON FOREST SUCCESSION FOR LOCAL LAND MANAGEMENT

A paper in preparation for submission to *Global Change Biology*, co-authored with Scott D. Brigham, Ronald P. Neilson, John P. Bolte, David R. Conklin, Dominique Bachelet, Peter J. Gould, Constance A. Harrington, Jane Kertis, James Merzenich, Cody Evers, and Bart R. Johnson.

Introduction

Human activities dominate and alter terrestrial ecosystem dynamics through both anthropogenic climate change and land-use change, among other factors (Vitousek et al., 1997). Changes in land use incur benefits and costs that accrue at different time-scales (Farber et al., 2006) contributing to complex feedbacks between human activities and ecosystems in space and time. Projecting the interactive effects of climate change and land-use decisions is therefore crucial to managing ecosystems. To do so effectively requires mechanistic simulations of climate change, land management, ecological succession, and disturbance at a fine spatial grain commensurate with the scales at which human decision making takes place. Our research objective was to explore how changes in climate and land use policy might interact to affect wildland fire and ecological succession. In particular, we sought to identify how these factors might operate at the landscape scale to affect the conservation and restoration of critically imperiled oak savanna ecosystems. In this paper we describe the development of a new modeling tool that incorporates information from several different classes of models, and yields annual spatially-explicit maps of vegetation at a fine spatial grain. To demonstrate model sensitivity and behavior, we apply this model to an area of wildland-urban interface in the southern Willamette Valley, Oregon, USA.

Dynamic global vegetation models (DGVMs) have emerged as a leading and accepted way to evaluate the potential for changes in vegetation under future climate change scenarios (Kucharik et al., 2006; Gavin et al., 2007; Littell et al., 2010). These

models are diverse, but in general include biogeochemical, physiological, and disturbance mechanisms to simulate changes in vegetation (Moorcroft, 2006). DGVMs have also been used at regional scales to provide public and private land managers with better information on potential changes in vegetation (Koca et al., 2006; Rogers et al., 2011). To be globally applicable, however, DGVMs must simplify their representation of vegetation and landscapes. Most DGVMs describe vegetation in broad physiognomic groups, rather than specifying individual plant species (Bachelet et al., 2001). While some DGVMs may include management (Albani et al., 2006), management is not simulated mechanistically based on human decision processes. In addition, most DGVMs also use a spatial grain that is coarser than the spatial grain at which land-use decisions are made (Hurt et al., 1998).

Plant community structure and composition is the dynamic product of plant growth and mortality, non-anthropogenic disturbances, and human influences. To the extent that DGVMs simulate these processes only coarsely, non-mechanistically, or not at all, their projections are likely to diverge from observed vegetation. Furthermore, DGVMs that must “spin-up” to equilibrate carbon and nutrient pools may provide projections that further diverge from observed vegetation if their initial vegetation type does not match that of the current landscape. For these reasons, coupling DGVM projections with models that operate at a fine spatial grain, use observed current vegetation as a starting point for future simulations, and allow the incorporation of mechanistic land management, would substantially advance simulations of climate change impacts on vegetation in human-dominated landscapes.

To explore how changes in climate and land use policy might interact to influence vegetation dynamics, we developed a new modeling tool, Climate-sensitive Vegetation State and Transition Model (CV-STM). The new model integrates components and outputs from four modeling systems to simulate the interactions of climate change and human land use decisions on ecological succession. CV-STM (1) simulates changes in vegetation productivity and plant physiognomic type based on changes in climate, (2) links the resultant plant physiognomic types to locally relevant plant community types in terms of tree species composition and vegetation structure, (3) allows for growth of, and competition among, tree species to drive vegetation succession, and (4) supports

mechanistic simulations of human land-use decision making. The resulting model is spatially explicit and probabilistic, while retaining deterministic future climate and physiognomic vegetation class forcing. Repeated simulations with the model allow for exploration of a range of potential future conditions. In the following section, we describe the development of CV-STM and its components. We then describe a series of experimental simulations using CV-STM that test its functionality across a range of climate change scenarios and levels of landscape disturbance.

Model Design

CV-STM draws upon existing models that we modified substantially, and incorporates them within a highly adaptable state-and-transition modeling framework (Figure 4.1A). More detailed descriptions of the model components are given in the following subsections. Descriptions of the modifications that we made to these components, and how we parameterized them for our specific study area, are provided in the Model Parameterization section.

Spatial Framework

To include mechanistic and spatially explicit land-use decision making, we built CV-STM to operate as a vegetation model within Envision. Envision is an agent-based model of landscape change that operates within a geographic information system (GIS) environment (Bolte et al., 2006; Guzy et al., 2008). The central feature of Envision is a spatially explicit model of human decisions that can be linked to models of other processes.

The spatial grain at which agents make decisions in Envision is referred to as an integrated decision unit (IDU), which in our use is the GIS polygon defined by the intersection of the soil phase and taxlot parcel boundaries, using ArcGIS (ESRI, 2009). Each IDU is assigned an “agent,” who controls decisions about the IDU’s land use and management. Envision applies decisions to these IDUs probabilistically based on the parameterized preferences of different agent types. Agents make choices based on a set of actions (termed policies) that are available to them, their decision preferences, and feedbacks from the changing landscape, thus allowing for the emergence of complex

model behavior. An IDU's vegetation type can change due either to an agent decision, ecological succession, or wildfire.

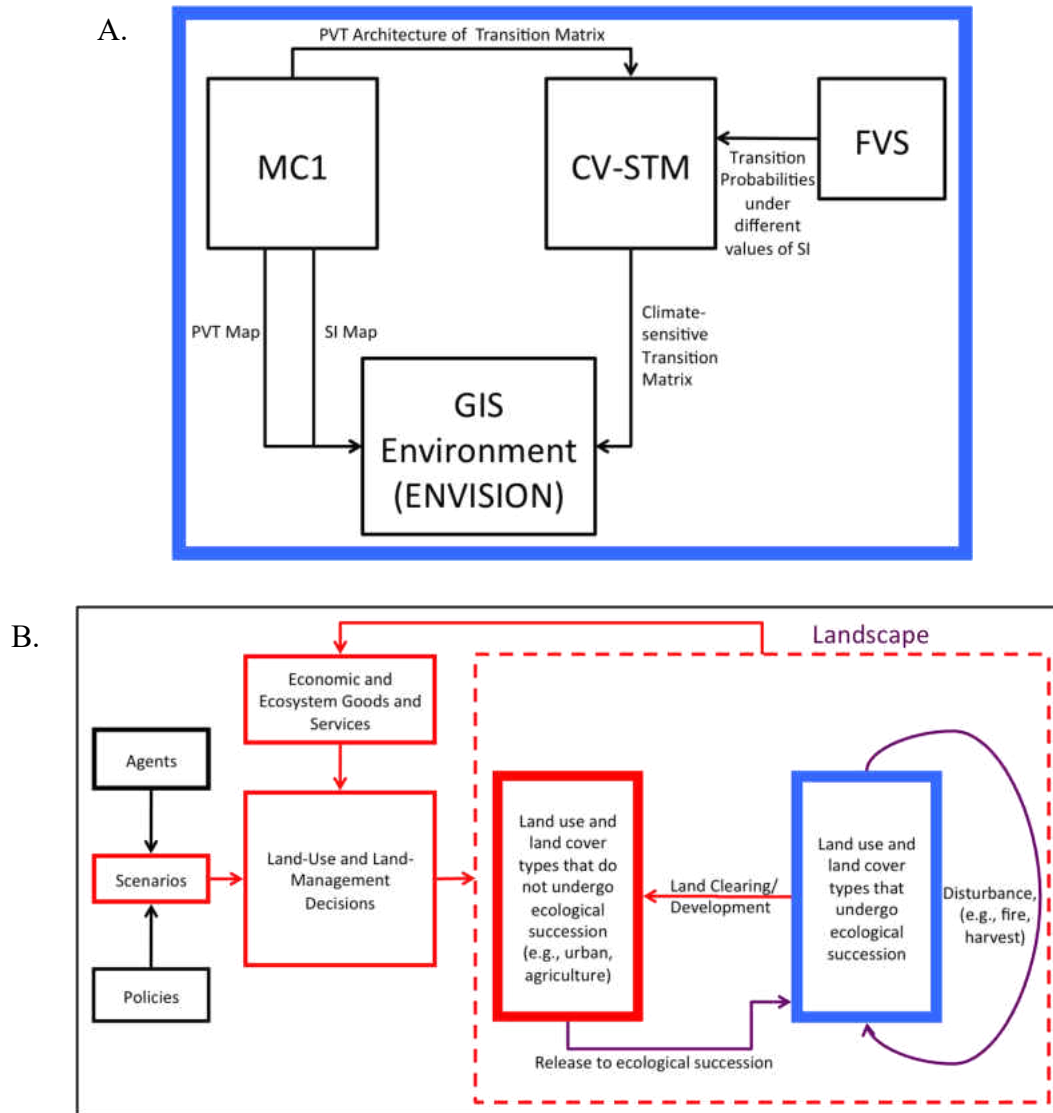


Figure 4.1. Schematic diagram of CV-STM coupled with MC1, FVS, and Envision (4.1A). 4.1B Shows the role of the coupled vegetation modeling from 4.1A (contained within the purple box) within the larger land-use decision model. PVT = Potential Vegetation Type, SI = Site Index, CV-STM = Climate-sensitive State and Transition Model, GIS = Geographic Information System. FVS, MC1, and Envision are existing computer models.

Previous implementations of Envision tracked successional changes with a rudimentary state and transition model (STM). We therefore constructed a much more complex STM as a new module in Envision to achieve our research objectives. While the coupling of agent-based decision making with a vegetation model is a central part of our larger modeling framework (Figure 4.1B), in the current paper we focus on the vegetation modeling component, which is capable of running independently from the GIS environment and agent-based land-use decision module in Envision.

Plant Community Definitions

STMs are relatively simple conceptual depictions of dynamic systems that can be reduced to a finite number of discrete conditions. STMs are commonly used in both highly theoretical settings, such as formal mathematics, and in highly applied settings, such as forestry (Haefner, 2005). For this project, we modified an existing STM framework developed for classifying vegetation types using the program VDDT, which is widely used for applying STM techniques to ecological management (ESSA Technologies, Vancouver, BC, Canada, www.essa.com). Plant communities may be defined by whichever features the users deem important and for which data are available. We defined plant communities based on dominant and subdominant tree species, mean stem size, canopy closure, and canopy layering, as is common in forestry applications.

Transition Probability Initialization

Different combinations of empirical data and expert judgment may be used to initialize transition probabilities in an ecological STM (Bestelmeyer et al., 2003). We used the Forest Vegetation Simulator (FVS: Crookston and Dixon, 2005) to generate the initial transition probabilities for the STM based on plot-level data from a large number of forest stands. FVS is widely used among foresters in the United States, and variants exist for most regions of North America. FVS predicts tree growth based on regionally-defined statistical relationships. It uses lists of trees in combinations of species and size classes, as both input and output. Although small probabilistic variations in tree growth and mortality occur in the course of an FVS run for a given tree list, the basic successional trajectory remains the same. By using multiple tree lists to parameterize

transitions from each state, the plot-level variability of known stands could be incorporated using a transition probability list, thus allowing a wide array of possible transitions for any given state. In FVS, tree growth, mortality and competition are based on site index (SI), which is the height to which a tree grows in 50 years. Because this approach assumes that the recent historical growth rate of an individual tree is the only predictor of its growth, it is insensitive to changes in climate.

Transition Probability Modifications and Emergence of Novel Communities

Because FVS assumes a stationary climate, it was necessary to invent a method to bring a climatically non-stationary DGVM, MC1 (Bachelet et al., 2001; Lenihan et al., 2003), into a climatically stationary, FVS-trained STM. We developed techniques to adjust the transition probabilities to reflect changing climate effects on stand composition and tree growth rates using estimates of productivity and potential plant community types from MC1. MC1's projections are sensitive to changes in input variables (e.g., temperature, precipitation, and humidity projections from climate models, and soils data), model parameters (e.g., sensitivity of productivity to changing atmospheric CO₂ concentration), and emergent properties (e.g., fire disturbance regime and nutrient availability). The current implementation of MC1 in the northwest United States is on a 30 arc-second grid, which translates to approximately 800-m grid cells (Rogers et al., 2011). The fire sub-model within MC1 (Lenihan et al., 1998) distributes the carbon pools into fuel categories, calculates the moisture content of these fuels, and then removes carbon from the appropriate pools on a cell-by-cell basis. MC1 uses spin-up and equilibration phases with de-trended historic climate data, a historical period with observed climate data, and then provides projections of the potential vegetation for each pixel in the landscape at each time-step in the future based upon data from general circulation models. MC1's projection of potential vegetation type (PVT) is based on broad physiognomic types (e.g., temperate maritime evergreen needleleaf forest), which we interpreted in terms of community types and dominant tree species in our study area. We used these projections of PVT to (1) identify species and community types that might become dominant locally under climate change, and (2) to constrain the STM to use only a subset of the full suite of transitions in the model for a particular MC1 grid cell and

time step. We also used correlations between MC1 output and site index (SI) to dynamically adjust SI annually for each Envision IDU, a second mechanism that modified transition probabilities.

Design Summary

Our modeling approach (CV-STM) incorporates climate-driven changes in tree growth potential (as SI) and community types (as broad plant physiognomic groups) by combining information from three other models, MC1, FVS and VDDT, to create a table of transition probabilities. CV-STM allows for finer description of local plant communities than DGVMs, uses current vegetation as the starting point for future projections, uses large local datasets for parameterization of transitions, allows for the incorporation of various land-uses, and achieves all of this at a fine spatial grain that is appropriate for informing local management decisions (Figure 4.1). Transitions within CV-STM were initially trained by FVS using a large local database. CV-STM can then operate as a module within Envision, along with space- and time-filling maps of MC1 output for PVTs and projected SI, and thus incorporate spatially explicit effects of climate change on successional transitions in a landscape. In this paper, CV-STM uses Envision as a GIS framework to provide climate-sensitive spatial input data. However, if the full capabilities of Envision are used, simulations of vegetation change can be coupled to mechanistic simulations of wildland fire behavior, other ecological disturbance processes, and to agent-based human decision modeling (Figure 1B). In this fully coupled model, feedbacks from ecosystem services and economic goods provided by the landscape can influence agent behavior, which in turn affects the landscape. A description of this fully coupled model will be the subject of future publications.

This model design can be applied to many areas. While we chose certain existing modeling tools to meet our needs, there are many ways to parameterize an STM to achieve different objectives. Our approach should provide a useful framework for other researchers who seek to develop a model that can change vegetation using descriptions of forest community composition that include dominant and sub-dominant species, the current vegetation as a starting point for simulations, a fine spatial grain, and responses to changing climate and human land-use decisions. In the following sections, we describe

our study area, and the methods used to parameterize these model components for that particular study area.

Study Area

Our study area is located in the southern Willamette Valley, Oregon (Figure 4.2). The 820-km² study area is bounded by the Eugene-Springfield Metropolitan Area's urban growth boundary (population 256,000) and the edges of the Willamette Valley Ecoregion (Hulse et al., 2002). It encompasses three incorporated towns ranging from 1,000-8,000 people each, as well as extensive wildland-urban interface. The study area includes approximately 20,000 taxlot parcels divided into approximately 89,000 IDUs; the maximum mapping unit is 5 ha and the vast majority of IDUs are 1 ha or less. Elevation ranges from about 115 m to 630 m from the Willamette Valley bottom to the foothills of the Cascade Mountains (Figure 4.3). Extant vegetation includes diverse successional vegetation types, ranging from prairie, savanna and woodland to forest, as well as agricultural lands.

Within the Pacific Northwest, conservation and restoration of open Oregon white oak (*Quercus garryana* Douglas ex Hook.) habitats is emerging as a conservation priority (Ulrich, 2010; Michalak, 2011). Oregon white oak savanna was once widespread throughout this area due to natural fire and Native American burning (Habek, 1961; Christy and Alverson, 2011), but oak savanna that retains both its open canopy structure and a significant component of its formerly diverse native ground layer occupies no more than 5-10% of its pre-Euro-American settlement area in the Willamette Valley Ecoregion. Losses have been primarily due to changes in land use, and succession to dense woodland and forest (Hulse et al., 2002) that are dominated by Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) due to reduction in fire frequency following Euro-American settlement circa 1850 (Morris, 1934; Habek, 1961). The oaks in these stands are often declining in their health and abundance (Clements et al., 2011).

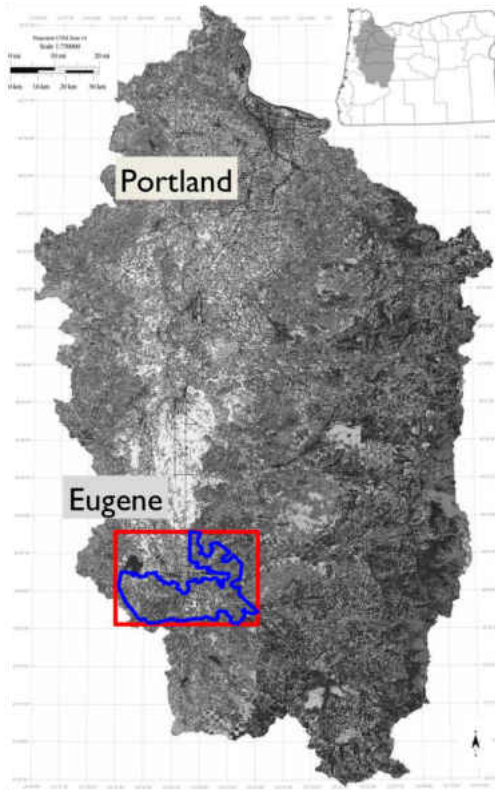


Figure 4.2. Study area location in the Willamette Valley, Oregon, USA. The red rectangle represents the bounding box for the MC1 simulations. The blue line surrounds the study area.

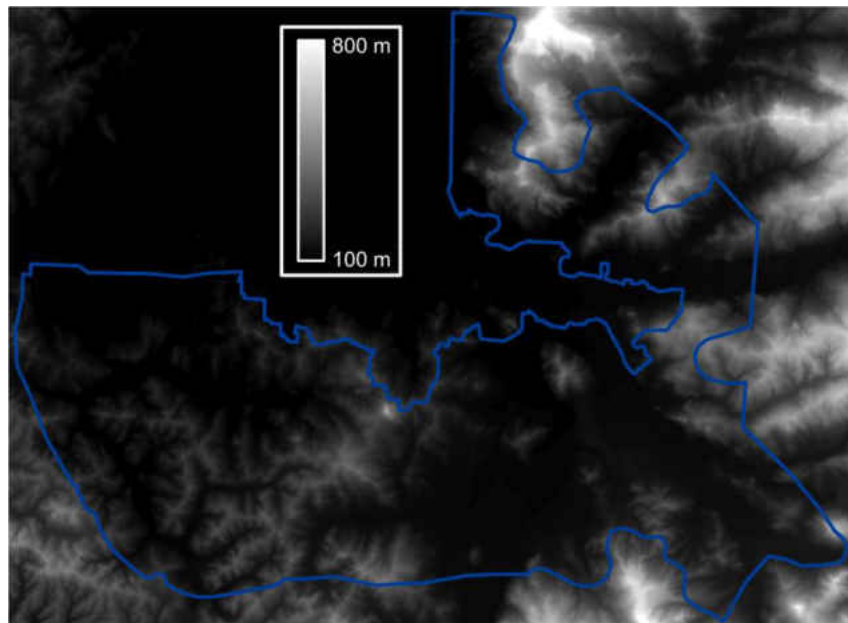


Figure 4.3. Elevation for the study area. The blue line surrounds the study area.

Model Parameterization

State and Transition Model

We created a customized STM to describe both current and potential future vegetation for the study area at a level of detail that would allow us to simulate the successional trajectories of open oak communities. We reduced diverse species and species assemblages by grouping species that were ecologically related into cover types defined by dominant and subdominant tree species, relying on previous fieldwork (Day, 2005; Sonnenblick, 2006; Murphy, 2008) and knowledge of these communities. Based on the projections of potential vegetation from previous work with MC1, we added three cover types to the STM (pine woodland, madrone woodland and forest, madrone and Douglas-fir forest) that are not dominant in the current landscape but that could become dominant under changing climate (Table 4.1). Ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) and Pacific madrone (*Arbutus menziesii* Pursh) occur in current forests in our study area in scattered locations at low abundances but are never community dominants. We describe each current and future community type using species that already occur in the study area and appear to be likely potential components of future communities. The distribution of Pacific madrone includes subtropical climate zones, and Ponderosa pine is representative of a conifer in a continental climate. A unique feature of our study area is its location near the confluence of three different climatic regions: maritime temperate, continental temperate, and subtropical. This location makes the increasing prominence of madrone and ponderosa pine plausible over the coming century. New species could migrate into our study area (or escape from horticultural plantings), but we assumed that the timeframe of our simulations (93 years) was too short to allow for the immigration and emerging dominance of new tree species.

We used 111 discrete states in 12 cover types and linked each cover type to the potential vegetation types from MC1 (Table 4.1). To define states, we used four parameters: dominant species, quadratic mean stem diameter (QMD), canopy closure, and canopy layering. QMD is a weighted mean that emphasizes larger trees in a stand, which is generally of greater utility in forestry. QMD groups were: no QMD, trees < 1.37 m tall; 0-12.7 cm diameter at breast height (DBH, 1.37 m); 12.7-25.4 cm DBH; 25.4-50.8

Table 4.1

State-and-transition model (STM) tree cover types with dominant and associated local species

<i>STM Cover Type</i>	<i>Dominant Species Description</i>	<i>Dominant Species</i>	<i>Associated Species</i>
Oak savanna	Drought-tolerant broadleaf deciduous	<i>Quercus garryana</i>	<i>Quercus kelloggii</i>
Oak woodland	Drought-tolerant broadleaf deciduous	<i>Quercus garryana</i>	
Oak and Douglas-fir woodland	Drought-tolerant broadleaf deciduous and needleleaf evergreen	<i>Quercus garryana, Pseudotsuga menziesii</i>	
Douglas-fir and oak woodland	Drought-tolerant broadleaf deciduous and needleleaf evergreen	<i>Pseudotsuga menziesii, Quercus garryana</i>	
Douglas-fir forest	Less mesic needleleaf evergreen	<i>Pseudotsuga menziesii</i>	<i>Calocedrus decurrens Pinus ponderosa</i>
Douglas-fir and maple forest	Mesic needleleaf evergreen and broadleaf deciduous	<i>Pseudotsuga menziesii, Acer macrophyllum</i>	<i>Thuja plicata, Tsuga heterophylla</i>
Douglas-fir and grand fir forest	More mesic needleleaf evergreen	<i>Pseudotsuga menziesii, Abies grandis</i>	
Bigleaf maple forest	Mesic broadleaf deciduous	<i>Acer macrophyllum</i>	<i>Alnus rubra and A. rhombifolia, Fraxinus latifolia, Populus balsamifera</i>
Pine savanna	Xeric evergreen needleleaf	<i>Pinus ponderosa</i>	
Pine woodland	Xeric evergreen needleleaf	<i>Pinus ponderosa</i>	
Madrone woodland and forest	Evergreen broadleaf	<i>Arbutus menziesii</i>	
Madrone and Douglas-fir forest	Evergreen broadleaf and needleleaf	<i>Arbutus menziesii, Pseudotsuga menziesii</i>	

cm DBH, and >50.8 cm DBH. Canopy closure categories were < 25%, 25-60%, and > 60% canopy closure. We defined the canopy to have either one or two layers. (STM development is described in greater detail in the supplemental materials.)

To assign states to the initial landscape, we collected descriptions of vegetative cover from multiple data sources, including the Gradient Nearest Neighbor (Ohmann and Gregory, 2002), Oregon Gap Analysis Program (“Existing Vegetation: NW ReGAP,” 2011), Land Use Land Cover (Hulse et al., 2002), Northwest Habitat Institute (“Northwest Habitat Institute,” 2011), 1851 Vegetation (Hulse et al., 2002). These sources were necessary to generate a list of trees, grouped by species, size class, canopy closure, and canopy layering, that accurately describe extant vegetation, especially prairie and oak savanna habitats of limited current distribution. Although the Gradient Nearest Neighbor dataset was the only one that specified each of the required four parameters, it was not developed for the fine-scale vegetation assignments that we implemented in this project and required substantial reclassification from other data sources to better reflect existing vegetation.

In order to rectify the often-conflicting spatial distributions and descriptions of vegetation in the available data sets, we used a logical rule-set that gave us one state for each IDU on the landscape. We created a 30-m grid representation of each data source and then prioritized them based on our on-the-ground knowledge of which were most accurate in particular situations (Day, 2005; Sonnenblick, 2006; Murphy, 2008; Yospin et al., 2012) and consultation with regional ecologists. We then assigned the state that had the largest plurality within each 30-m grid cell to that grid cell, aggregated the grid cells into their respective IDUs, and assigned each IDU the initial state that corresponded to the plurality of its constituent 30-m cells. We validated our results for several subareas of the study area using detailed field data from The Nature Conservancy that had been mapped in GIS. (See supplemental materials for a more detailed description of the states.)

Transition Probability Initialization

To generate transition probabilities for our STM, we used the rates of tree growth and successional changes projected by a revised version of the Westside Cascades variant of FVS with substantial modifications to the height, growth rate, competitive dynamics,

and mortality of Oregon white oak (Gould et al., 2011). The model was run using multiple tree lists to initialize and train the transition probabilities in our STM. Tree lists came from 2,092 plots from several data sets, including from a previous project (Johnson et al., unpublished data), the Gap Analysis Project plots (“Existing Vegetation: NW ReGAP,” 2011), the Pacific Northwest integrated database (Hiserote and Waddell, 2005), and the Pacific Northwest Forest Inventory Analysis annual inventory (USDA Forest Service, Forest Inventory and Analysis, 2010). The tree lists were binned into states from our STM by assigning each tree list to a state on the basis of species dominance, mean stem diameter, stem density, and canopy layering, as defined in the STM. Runs were performed with and without tree regeneration. Tree regeneration was simulated by adding seedlings into tree lists every 10 years based on the number and species of seedlings in 1,380 plots with seedling inventories. To add tree seedlings to a state and simulate regeneration, we randomly selected and averaged five inventoried seedling plots from the subset of plots that corresponded to the cover-type of the state for which we were simulating regeneration. We ran each of these tree lists for one hundred years at site index (SI) values from 15.24 m to 45.72 m, by increments of 3.05 m, and then re-binned the output tree lists into STM states. Our use of multiple tree lists for each state resulted in many possible successional trajectories in FVS, from which we extrapolated the values of annual transition probabilities. We used a range of SI values in FVS that was larger than we expected to find in the current and future landscapes to ensure that we would be able to adjust transition probabilities without exceeding the boundaries of a regression relationship between SI and MC1 output (described below).

Transition Probability Adjustments and Constraints

MC1 Customization

MC1 takes several thousand years of simulation time with de-trended historical climate data to equilibrate carbon and nutrient pools during the spin-up phase. These pools then provide the basis for simulations through a period of observed historical climate data, in our case from 1895 through 2006. The end of this historical period then becomes the beginning of the future simulation period. Standard implementation of MC1 yielded a historical period that began with temperate maritime evergreen needleleaf forest

(which we equate to Douglas-fir forest) instead of the prairie and savanna habitats observed for the study area (Habek, 1961). It is likely that the emergent fire behavior regime in MC1 drastically underestimated the historical fire frequency because of recurring burning by indigenous people (Christy and Alverson, 2011). To explore the consequences of this underestimation, we built new adjustable parameters into MC1 that allowed us to specify the fire return interval in years and the burn date by Julian day. We then examined MC1 output variables using fire return intervals of 3, 5, 10, 15 and 20 years, at Julian days from 150 to 300 by steps of 25 days (appropriate for fire season of the region's Mediterranean climate) during the spin-up phase. Variable burn days allow for fires that consume different amounts of the available fuels, as does the variable fire return interval.

We found that many combinations of fire return interval and burn day created vegetation conditions that were similar to observed vegetation in the study area prior to Euro-American settlement. We chose to use a 10-year fire return interval, burning on Julian day 197, during the spin-up phase. We then simulated the historical period with fire disabled in the model to mimic both the loss of indigenous burning and active fire suppression that occurred in the study area. Only a few years after removing fire from the system, vegetation in the MC1-simulated study area quickly approached values associated with a dense Douglas-fir forest, matching observations of the directions of successional change, albeit with changes occurring more rapidly than actually transpired. These experiments validate the functionality of the fire and vegetation models in MC1, while highlighting the rapidity of change within MC1.

We disabled the fire model in MC1 to simulate the future period, except in the following section where we wanted to explore the full range of MC1 outputs. We did so (1) to distinguish direct climate effects on vegetation from interactive effects with disturbance, and (2) to incorporate a different mechanistic fire model, FlamMap (Finney, 2006), that will operate at the spatial grain of our IDUs and with fuels parameters derived from our community types rather than from MC1 PVTs (Sheehan, 2011). This will allow wildfire and human management to interact with CV-STM within Envision.

MC1 Future Projections

We explored the dynamics of three general circulation models (GCMs) – Hadley (Johns, 2003), MIROC (Hasumi and Emori, 2004), and CSIRO (Gordon, 2002), all run under the A2 emissions scenario (Nakićenović, 2000). Recent developments make it unlikely that human emissions will be less than the A2 emissions scenario (Raupach et al., 2007). We also explored the effect of CO₂ fertilization in MC1 on future vegetation dynamics. Thus, we examined six future climate scenarios – three GCMs crossed with two CO₂ fertilization parameterizations. Analysis of the output under varying CO₂ fertilization scenarios indicated that, within the study area, MC1 was insensitive to changing vegetation sensitivity to CO₂ fertilization (see the supplemental materials for further details). Thus, despite findings showing the importance of CO₂ fertilization in many regions (Norby et al., 2005), further analyses in this manuscript consider only the three GCMs using the A2 emissions scenarios and moderate vegetation sensitivity to atmospheric CO₂. We refer to these three combinations of GCM, CO₂ emissions, and vegetation sensitivity to CO₂ as climate scenarios.

MC1 output showed modest trends over time in variables associated with productivity. Over 90 years of simulation time, carbon pools generally changed by 5 to 10%. In contrast, MC1 showed large changes in potential vegetation types. At simulation year 0 (2007 AD), the study area was a mix of three PVTs. The dominant PVT (about 85% of the landscape) was temperate maritime evergreen needleleaf forest in the bounding rectangle around the study area (Figure 4.4), which we interpret as representing Douglas-fir forest (Table 4.1). About 15% of the area began in the subtropical mixed broadleaf and needleleaf evergreen forest, which can be interpreted as representing mixed Douglas-fir and oak or madrone forest. There were also six grid cells (~ 0.2% of the landscape) that were projected to be C3 grassland. These remained as C3 grassland for all climate scenarios, at all time points. The shallow soils of the input data for these MC1 grid cells constrained their dynamics with respect to potential vegetation types. The rapid and dynamic flux among vegetation types stems from the study area location, near the confluence of three distinct bioclimatic zones (Kuchler, 1965), and from the sensitivity of MC1 to projected climate changes in the study area.

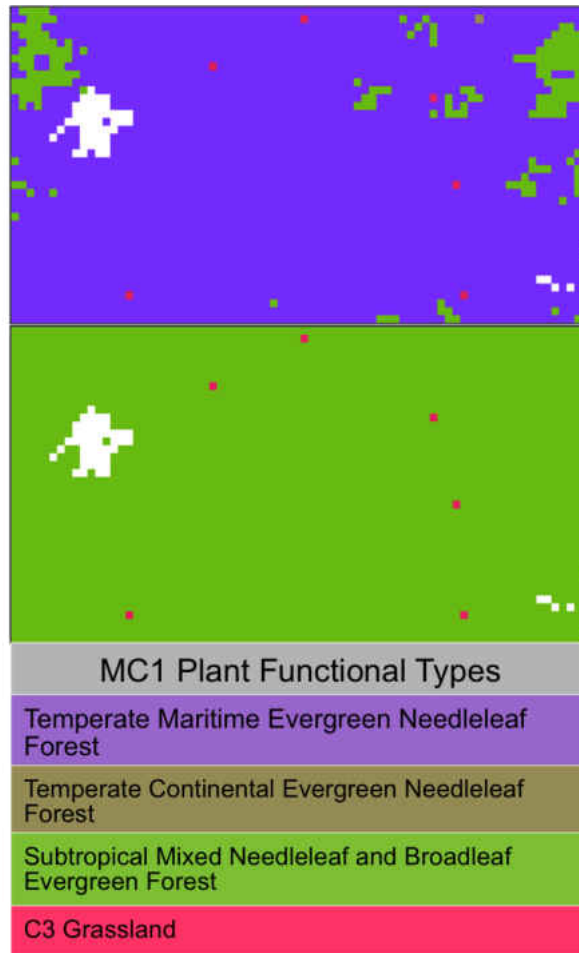


Figure 4.4. The dynamic global vegetation model MC1 potential vegetation types at Year 0 (top, 2007) and Year 90 (bottom, 2097) under the Hadley A2 global circulation model. Pixels in white have no data.

The time to reach the final PVT in MC1 depended on the GCM. All simulations showed some degree of switching between the subtropical mixed broadleaf and the maritime evergreen needleleaf forest potential vegetation types. When using the Hadley model, the landscape also substantially included the continental needleleaf evergreen forest potential vegetation type, mostly between simulation years 30 and 50. All models settled on the subtropical mixed broadleaf and needleleaf evergreen forest potential vegetation type by the end of the simulation period in 2099 (Figure 4.4).

With fire turned on, MC1 showed three spatially large, low intensity fires near the end of the simulation period (2077 – 2099) for all climate scenarios. These fires did not alter MC1’s projections of PVT, and had only minor effects on MC1 output variables.

Running MC1 without its fire model removes one of the crucial links in the model between climate and vegetation. The finding that MC1 projects limited fire for the future period in the study area, with only minor effects on some MC1 output variables, indicates that our decision to turn the fire model off had only a minor effect on projections of PVT and MC1 output variables. Our decision to turn off the fire model in MC1, however, means that our reported results with MC1 will disagree with previous research using MC1 for regions that include our study area (Rogers et al., 2011).

Transition Probability Adjustments

MC1 output does not include site index (SI) but it includes numerous outputs related to vegetation productivity, edaphic factors and climate. To relate MC1 output variables to SI values (Figure 4.1A), we correlated averaged MC1 output from 1982-2006 with available SI data (Gould et al., 2011). We performed this correlation for 1790 MC1 cells, ranging from central to southern Oregon, in the Coast Range and valleys. We made this geographic choice to bracket the range of expected SI in the study area from the present until 2099, based on the prediction that future climate in the Willamette Valley will resemble current climate in southwestern Oregon (Rogers et al., 2011).

We used a wide range of potential MC1 output variables related to vegetation and climate to derive a relationship with SI. Multiple linear regression and classification and regression trees were used to explore and analyze the data. Ultimately, we selected a regression model by Akaike's Information Criterion (AIC: Akaike, 1974) after controlling for autocorrelation among independent variables. Regression with AIC between MC1 output variables and SI yielded a model that was statistically significant, explained substantial variance in SI, and was ecologically meaningful (Table 4.2) with an overall adjusted $r^2 = 0.55$. Using the regression equation from Table 4.2, we produced space- and time-filling maps of SI for our study areas.

Table 4.2

Variables used in the regression equation relating MC1 variables to site index. Leaf shape index ranges continuously from 0 to 1, where 0 corresponds to needle-shaped leaves, and 1 corresponds to broad leaves. The final equation had an intercept value of 75.6

<i>Variable</i>	<i>Coefficient</i>	<i>Standardized Coefficient</i>
Total Soil Carbon	9.081×10^{-4}	0.482
Forest Net Primary Productivity	1.699×10^{-2}	0.229
Average June Temperature	2.158	0.183
Aboveground Live Forest Carbon	1.962×10^{-4}	0.120
Leaf Shape Index	-0.1989	-0.0551

The spatial grain for MC1 is a 30 arc-second grid, which yields approximately 800-m grid cells. These MC1 grid cells are much larger than the IDUs, and thus the MC1-projected SI needed to be downscaled to individual IDUs. To do this, we adjusted the future SI of each IDU proportionally over time, based on that IDU's initial SI, the MC1 cell's initial SI, and the MC1 cell's projected future SI:

$$SI_{IDU_t} = SI_{IDU_0} \left(\frac{SI_{MC1_t}}{SI_{MC1_0}} \right)$$

where SI_{IDU_t} is the SI for a particular IDU at a point in time, SI_{IDU_0} is the initial SI of that IDU, SI_{MC1_t} is the SI of the MC1 cell at a point in time, and SI_{MC1_0} is the initial projected MC1 SI.

Transition Probability Constraints

Since the STM contains all vegetation types and transitions needed for multiple future climate scenarios, as well as the present climate, we limited the possible transitions as follows: 1) we determined which cover types and associated states and species would be compatible with each MC1 PVT, and 2) we constrained the STM to allow transitions only to compatible states (Table 4.3). For example, under the subtropical mixed broadleaf and needleleaf evergreen forest PVT, no transitions to pine savanna or woodland are allowed; existing pine savanna or woodland states can only remain unchanged, or transition to states via allowed transitions. Within each PVT, transition probabilities for each state were proportionally adjusted to compensate for the transitions that were disallowed so that the sum of allowed probabilities always equaled one.

Table 4.3

State and transition model (STM) tree cover types to which transitions are allowed under each MC1-derived potential vegetation type (PVT)

<i>STM Cover Type</i>	<i>Temperate Maritime Evergreen Needleleaf Forest</i>	<i>Temperate Continental Evergreen Needleleaf Forest</i>	<i>Subtropical Mixed Evergreen Forest</i>	<i>C3 Grassland</i>
Oak savanna	allowed	allowed	allowed	allowed
Oak woodland	allowed	allowed	allowed	
Oak and Douglas-fir woodland	allowed	allowed	allowed	
Douglas-fir and oak woodland	allowed	allowed	allowed	
Douglas-fir forest	allowed		allowed	allowed
Douglas-fir and maple forest	allowed			
Douglas-fir and grand fir forest	allowed			
Bigleaf maple forest	allowed			
Pine savanna		allowed		allowed
Pine woodland		allowed		
Madrone woodland and forest			allowed	allowed
Madrone and Douglas-fir forest			allowed	

As PVTs change in the future with climate change, we permitted all existing states to persist in the landscape until affected by a stand-replacing disturbance because individual trees are long-lived and can survive for many years in suboptimal growth conditions. There are many possible types of stand-replacing disturbance that are relevant in the study area, including fire, insect damage, and harvest. Following a stand-replacing disturbance, only transitions allowed under the current PVT may occur. If the dominant tree species in the pre-disturbance state is compatible with the current PVT (Table 4.3) and is capable of re-sprouting following disturbance, then the IDU will regenerate as a young tree state of the cover type corresponding to that species. Re-sprouting is the growth of new shoots from meristem tissue that may survive a stand-replacing disturbance, and is common in oaks, bigleaf maple, and madrone. If the pre-disturbance state did not contain any compatible species that re-sprout following disturbance, then the IDU regenerates as an open, grass/forb state of the dominant cover type for that PVT. For example, within the temperate maritime evergreen needleleaf forest PVT, an IDU that was mixed oak and Douglas-fir woodland pre-disturbance will regenerate as a young oak state. Under that same PVT, an IDU that was mixed Douglas-fir and grand fir forest will regenerate as a grass/forb state. We address the limitations of this approach in the discussion section.

Model Behavior

STM Probabilistic Behavior

We ran repeated simulations in CV-STM for 500 years, starting from either an oak savanna state or a Douglas-fir state, with $SI = 30.48$ under the maritime evergreen needleleaf forest PVT (Figure 4.5). Performing these simulations outside of Envision and non-spatially allowed us to examine the probabilistic nature of CV-STM. We performed these simulations in R (R Development Core Team, 2008) – for further details, see the supplemental materials). Results are consistent with observed successional trajectories (Habek, 1961; Thilenius, 1968; Johannessen et al., 1971; Day, 2005). Under the maritime evergreen needleleaf forest PVT, all simulations tended to converge on Douglas-fir forest as the final state. The model does not tend to yield a single climax state, but instead typically resulted in alternate states that were stable near the end of the 500-year

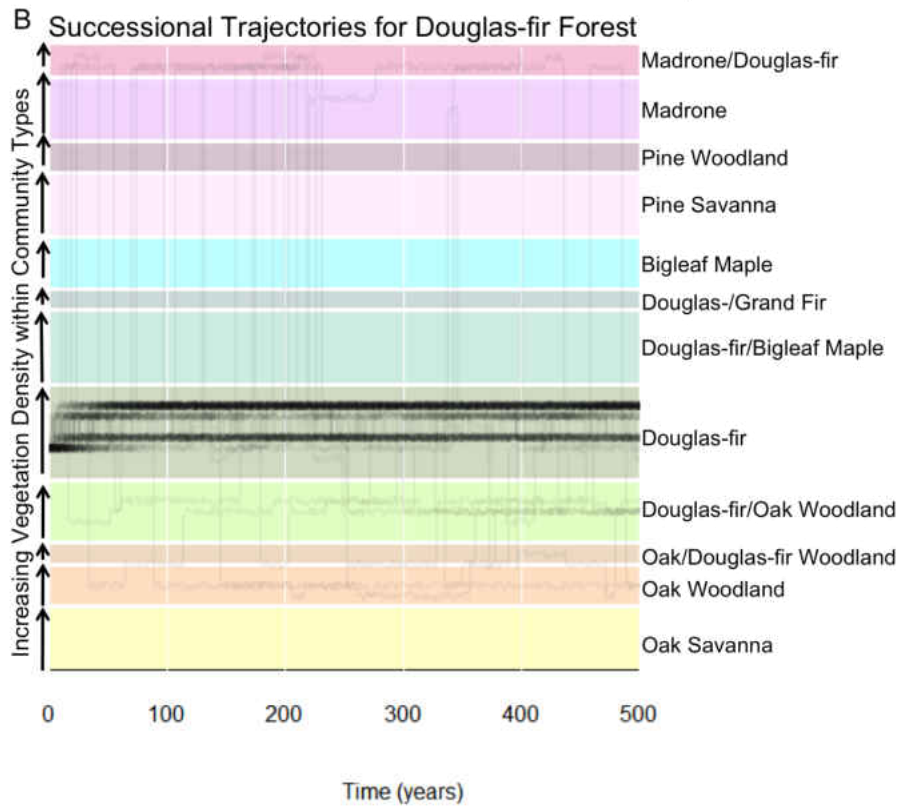
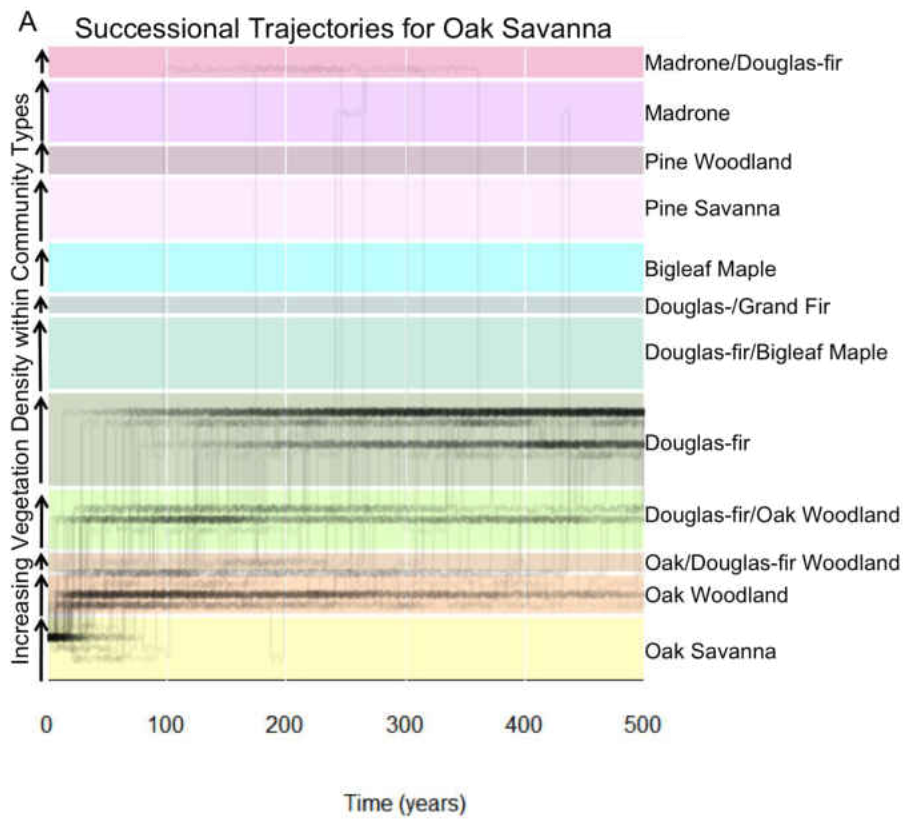
simulation. Oak savanna largely transitioned to oak woodland within 50 years, but while oak woodlands diminished in extent, they were able to persist throughout the simulation. Our field data and other research in this region suggest that succession from oak woodland to Douglas-fir forest may typically be somewhat faster than simulated by the model (Thilenius, 1968; Johannessen et al., 1971; Day, 2005). For all starting states, the tendency was to move toward a few different Douglas-fir forest states, differentiated by tree size and canopy layering. Some small amount of grand fir was usually present following the first 100 years of simulation time. Bigleaf maple and madrone types appeared infrequently and ephemerally. The model showed the capacity for states to both increase and decrease in mean stem size. These changes in QMD could reflect either infill with small trees, tree mortality, or individual tree growth, as projected by FVS.

Effects of Disturbance and Climate Change

Simulations were conducted with CV-STM running as a module within Envision to explore the effects and interactions of climate and disturbance scenarios at the landscape scale. We simulated four climate scenarios (no climate change, Hadley A2, MIROC A2, CSIRO A2) and three levels of generic, stand-replacing disturbance (no disturbance, 5% of the landscape/year, 17% of the landscape/year). These disturbance levels yield disturbance return intervals of 20 years and 6 years, which bracket the estimates of the pre-Euro-American fire return interval for the Willamette Valley Ecoregion (Morris, 1934; Weisberg and Swanson, 2001; Walsh et al., 2010). Fire was the dominant agent of disturbance in this landscape, so these disturbance levels were useful not only for testing model behavior, but also for comparison to historical observations. We implemented disturbance in a spatially random and disaggregated fashion, unlike any disturbance the landscape is likely to experience, in order to rigorously explore a wide range of potential model behavior. The interactions of this vegetation model with a mechanistic fire model and a mechanistic model of human land management decisions in fully coupled Envision runs will be the subject of forthcoming publications. This implementation of generic disturbance, however, allows us to explore the range of behavior that CV-STM produces when specific disturbance regimes are crossed with different climate scenarios.

Disturbance and climate interacted strongly to drive vegetation change in CV-STM (Figure 4.6). Without disturbance or climate change (Figure 4.6A), there was an overall trend in the landscape toward Douglas-fir forest at the expense of oak savanna, while oak woodland initially increased and then stabilized until the end of 90-year model run. As can be seen from the model running probabilistically for longer amounts of time (Figure 4.5), once the pool of oak savanna is exhausted, losses begin to accrue in oak woodland, until most of the landscape becomes various types of Douglas-fir forest. With sufficient disturbance, however, there was a stabilization or increase in oak savanna and an increase in bigleaf maple, accompanied by reduced increases to Douglas-fir forest and losses to oak woodland.

Figure 4.5 (following page). Changes in state and transition model (STM) cover types over time. Each panel shows 100 probabilistic simulations run for 500 years each from two different starting states. Colored boxes correspond to the twelve different cover types used in the STM, each of which contains all associated states – the height of the colored box corresponds to the number of states specified in the STM. Within each cover type, moving higher on the Y-axis corresponds to increased vegetation density, either in terms of stem diameter, canopy closure, canopy layering, or a combination of the three. Darker traces indicate a greater proportion of simulations in a particular cover type at a particular point in time. Simulations were conducted for $SI = 30.48$ under the maritime evergreen needleleaf forest PVT. Panel A begins in an oak savanna state, and ends with substantial proportions of: large diameter, closed canopy, one- and two-canopy layer Douglas-fir states; medium diameter Douglas-fir/oak woodland states; and medium diameter oak woodland states. Panel B begins in a medium diameter, one-canopy layer Douglas-fir state, and ends with substantial proportions of large diameter, closed canopy, one- and two-canopy layer Douglas-fir states.



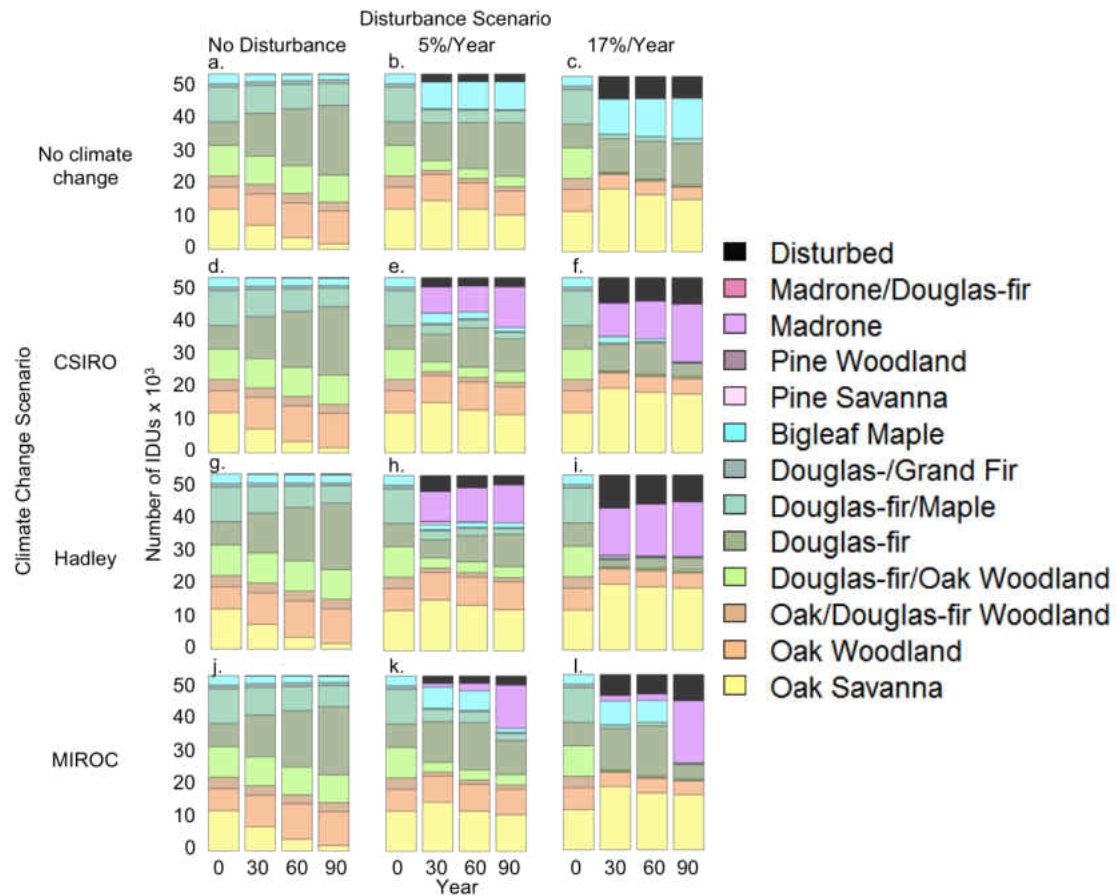


Figure 4.6. Projected STM cover types in number of Integrated Decision Units (IDUs) at four time points with three global circulation models. Descriptions of the cover types are in Table 1. Climate scenarios are no change (a-c), CSIRO A2 (d-f), MIROC A2 (g-i), and Hadley (j-l). Disturbance regimes are no disturbance (a,d,g,j), 5% disturbance per year (b,e,h,k), and 17% per year (c,f,i,l). The purple color that becomes common in panels e, f, h, i, k, and l corresponds to the madrone (M) cover type.

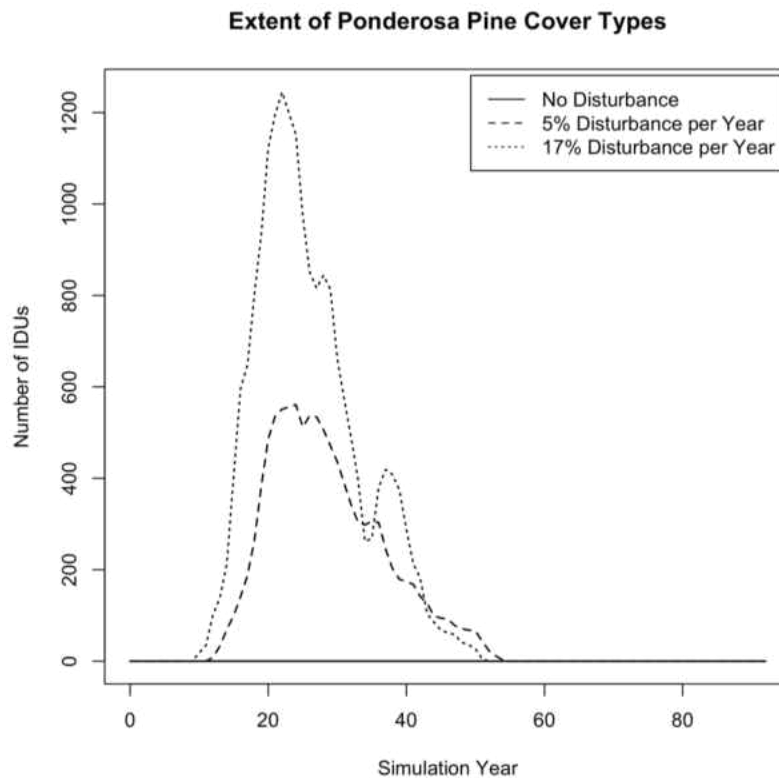


Figure 4.7. Extent of ponderosa pine cover types. Temporal dynamics under the Hadley general circulation model under 5% disturbance.

The effect of climate change was heavily dependent on disturbance, and in general, all climate scenarios produced similar changes in vegetation for any given disturbance scenario by year 90, the end of the simulation (Figure 4.6). Without disturbance, the climate change scenarios had little impact on vegetation. In contrast, under the shortest disturbance-return interval all of the climate change scenarios generated a large reduction in the amount of Douglas-fir forest by the end of the model run and increased the amount of novel local cover types (e.g., madrone) in the landscape. Oak savanna habitats increased with increasing disturbance regardless of projected climate change, and achieved somewhat higher quantities than under no climate change at comparable disturbance levels.

The interaction between disturbance and climate change also showed some of the nuances differentiating how the GCMs project climate change for the study area

(Bachelet et al., 2011; Rogers et al., 2011). While all three GCMs projected warming in the study area, Hadley and MIROC projected comparable warming ($\sim 4.2^{\circ}\text{C}$), while CSIRO projected less warming ($\sim 2.6^{\circ}\text{C}$). CSIRO showed the largest increase in mean annual precipitation, MIROC showed a smaller increase in mean annual precipitation, while Hadley showed a small decrease in mean annual precipitation (Rogers et al., 2011). Hadley produced the most rapid changes in vegetation when disturbance occurred in the landscape, with the largest increases in oak and madrone cover types. By the end of 90 years, however, the three models tended to converge. MIROC produced little change for most of the simulation time. The rate of vegetation change at the end of the MIROC simulations with disturbance, however, far exceeded the rates of change seen under the other combinations of climate and disturbance scenarios. Ponderosa pine appeared, but only very briefly, in two episodes during the simulation (Figure 4.7). At its greatest extent (under Hadley and the 17% disturbance regime), ponderosa pine cover types occupied approximately 1.5% of the IDUs in the study area.

Spatial Output

Given the spatially random and disaggregated nature of the disturbance used in these simulations, it is inappropriate to over-interpret the spatial output from the disturbance simulations. With this caveat in mind, however, the spatial output reveals important model dynamics (Figure 4.8). The initial landscape contained a mixture of oak, Douglas-fir, and bigleaf maple cover types (Fig. 4.8a). With a disturbance return interval of 6 years and no climate change, oak occurred largely on the lower slopes of the valley foothills, while maple largely occurred further upslope (cf. Figs. 4.3 and 4.8b). This result matches our ecological understanding of vegetation in lowlands for the study area under more frequent wildfire disturbance regimes (Johannessen et al., 1971). On the other hand, vegetation maps from 1851 do not show maple-dominated stands in the uplands, likely because wildfire was less frequent at higher elevations away from the valley floor. More recent observations show a strong maple presence and occasional dominance in uplands following disturbance by timber harvest (Johannessen et al., 1971); CV-STM matches this observation as well.

The strong interactions between climate change and disturbance were also apparent

spatially. Areas of the landscape that existed as Douglas-fir forest without a substantial oak component at the start of the simulation were almost entirely converted to madrone cover types (Fig. 4.8c). Much of the landscape, again, especially in the lowlands, remained in or changed to open oak savanna cover types, most likely because of the oak's ability to re-sprout following stand-replacing disturbance.

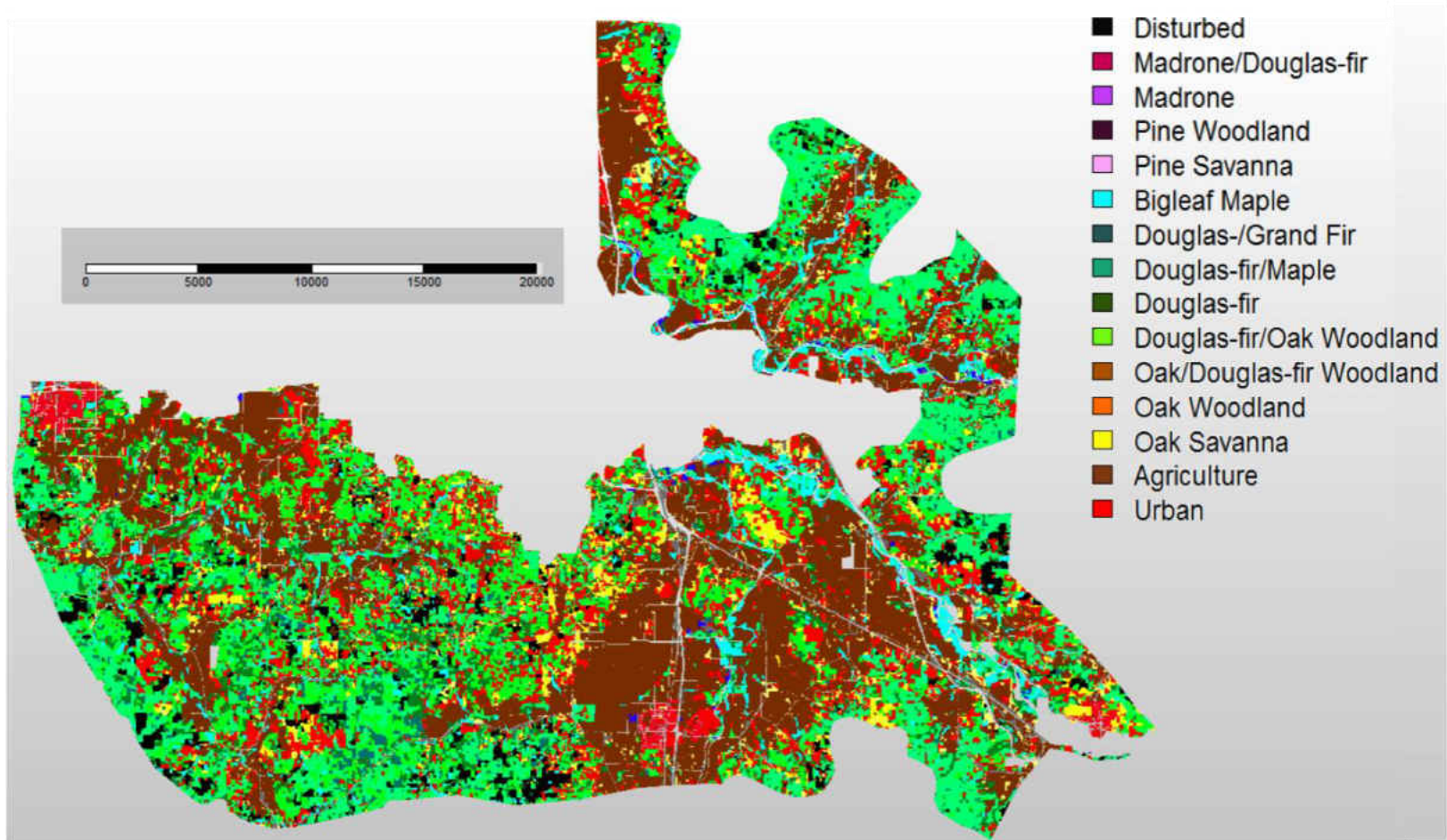
The simulations were performed only for areas that have "natural" vegetation at the beginning of the simulation in 2007. Many of the areas that were the highest quality oak habitat prior to Euro-American settlement have been converted to agricultural uses or urbanized, and are therefore not included in these (and previously discussed) simulations.

Discussion

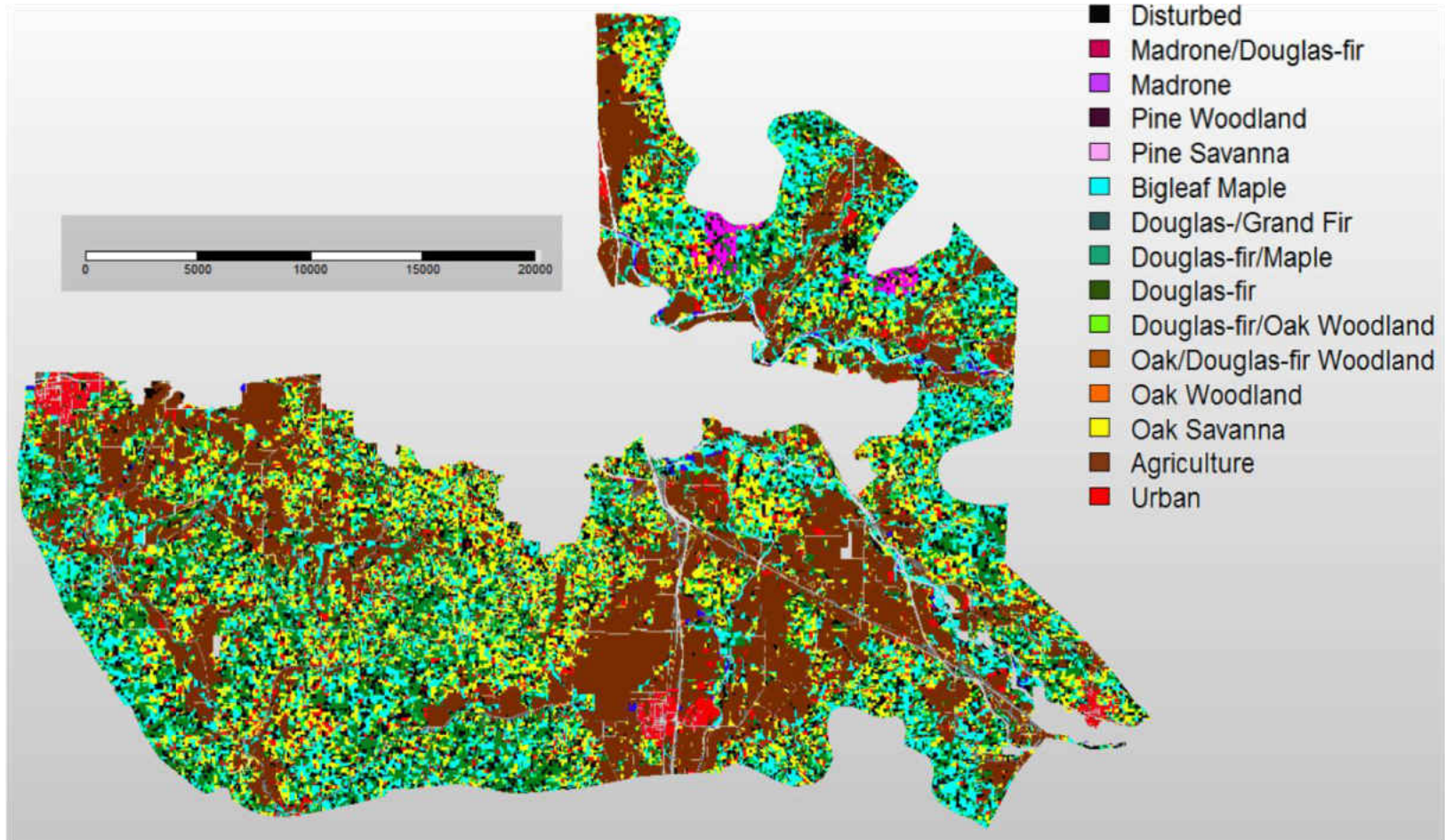
DGVMs are not designed to mechanistically simulate anthropogenic disturbance at a fine spatial grain, nor with time lags conferred by tree longevity. The likelihood that DGVMs can accurately predict disturbance and vegetation is remote in intensively human-managed landscapes such as the wildland-urban interface. CV-STM therefore provides a necessary bridge between DGVMs and land-use decision models.

Figure 4.8 (following pages). Simulated plant cover types shown spatially for the study area. (a) year 0, (b) No climate change, 17% disturbance, year 90, (c) Hadley A2, 17% disturbance, year 90. OA = Prairie and savanna, OW = Oak woodland, OD = Oak growing over Douglas-fir, DO = Douglas-fir growing over oak woodland, DD = Douglas-fir, DM = Douglas-fir mixed with maple, DG = Douglas-fir mixed with grand fir, BM = Bigleaf Maple, PS = Pine savanna, PW = Pine woodland, M = Madron, MD = Madrone mixed with Douglas-fir

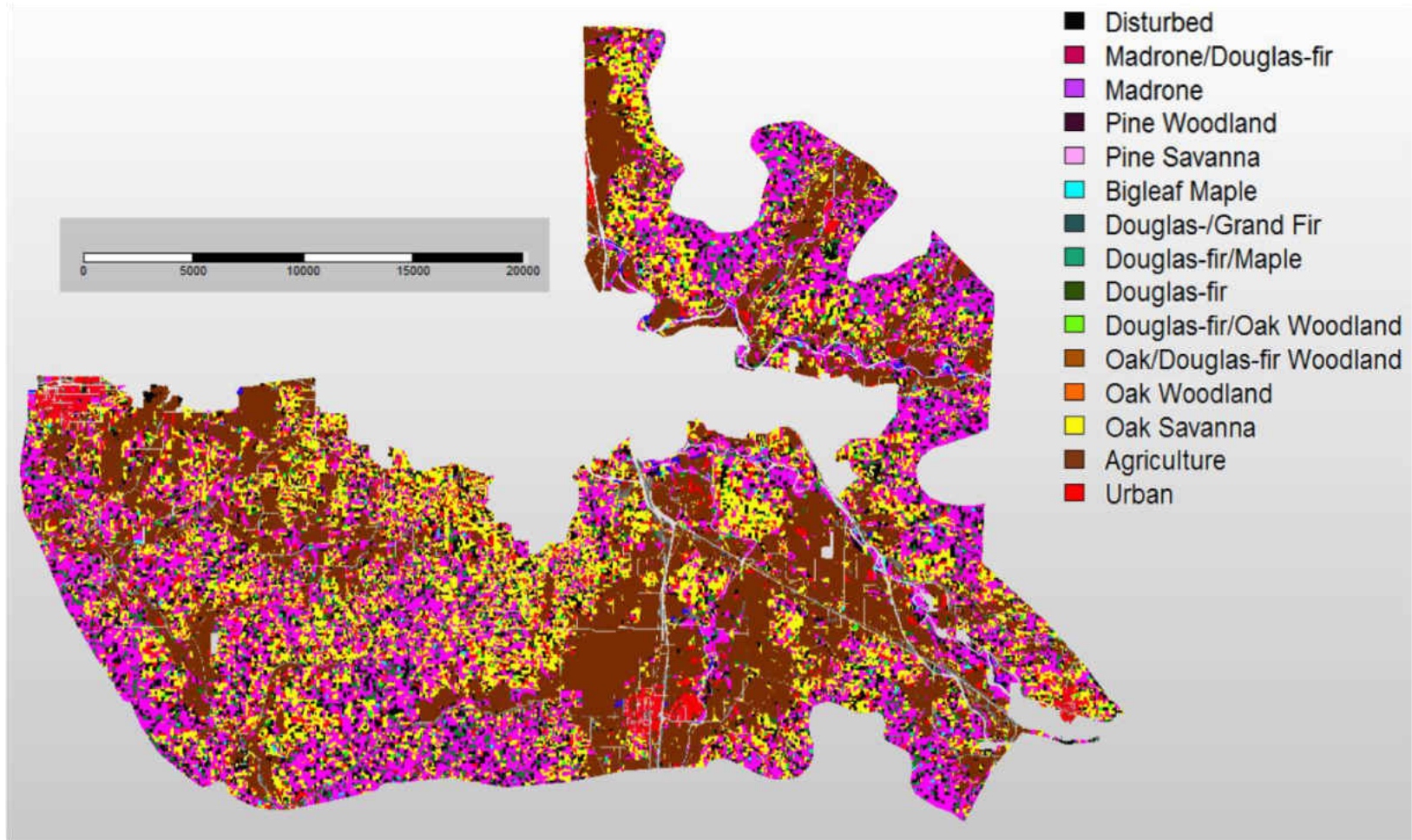
A



B



C



In some regions, a number of the important aspects of global climate change – for example, the sensitivity of vegetation to changing levels of atmospheric CO₂ – may have little effect, or may have their effects overwhelmed by other factors. This is particularly apparent in the minor differences among the three climate scenarios in this study, which differed in the timing of changes, but generally agreed on the direction and magnitude of changes by the end of this century.

We found a strong interaction in CV-STM between disturbance and climate change effects on vegetation, but our disturbance regimes were generic and did not incorporate potential climate effects on the disturbance regimes themselves. There are many means by which climate could interact with agents of disturbance, such as fire, insects, pathogens, mass mortality of trees through drought stress, or the interactions of multiple agents of disturbance with climate change. We explored MC1 output to look for evidence of widespread drought mortality and found none. Data were not available to parameterize CV-STM for specific agents of disturbance such as pathogen mortality, although fire will be included in fully coupled Envision runs in future publications.

CV-STM provides the expected dynamics with or without disturbance under current climate, suggesting that it appropriately depicts current vegetation dynamics. Under no disturbance, states from many starting conditions converge to Douglas-fir cover types under both current and future climate. Because CV-STM assumes that established forest stands persist under future climate, there are no dramatic changes in vegetation due to climate change without disturbance occurring. However, with stand-replacing disturbances, climate change results in increasing dominance of re-sprouting species. We have translated an increasing dominance of new MC1 PVTs as representing madrone and Ponderosa pine cover types, as these species occur in the current study area at low abundances and these cover types represent the nearest species assemblages that are representative of the new PVTs.

We cannot dismiss the possibility, however, that new dominant species more suitable to future climate will also arrive and establish. We used a DGVM, MC1, to guide our choices of physiognomic types and the geographic region within western Oregon from which we drew our tree lists. Because of this, CV-STM is limited to the types of guidance MC1 provides. For example, MC1 does not predict a shrub PVT in the study

area, but chaparral communities have been common in the study area at least as recently as the mid-Holocene Thermal Maximum, ca. 5K to 8K years ago (Detling, 1961), and still exist in isolated locations in the vicinity and in southern Oregon. With this in mind, we urge readers to interpret the model results cautiously; there are community types that could arise, and which CV-STM would not be able to predict. Our reliance on current species assemblages to parameterize successional transitions allowed us to incorporate realistic rates of successional change that began from the current vegetation, but at the cost of not identifying truly novel community assemblages. Nevertheless, we believe that our relatively short simulation period of 90 years limits the likelihood that species currently not in this region will successfully migrate here and become dominant. Beyond that 90-year period, this assumption will become less valid.

The rates of change in vegetative cover were much slower in CV-STM simulations than in MC1 simulations. There are two reasons for this. First, MC1 assumes that vegetation quickly reaches its maximum leaf area index as determined by water limitation, but transition rates in CV-STM were determined in FVS based upon regionally derived statistical relationships. Transition rates from the observed competitive dynamics that parameterize FVS are much lower than those imposed by physiological limitations in MC1. Second, successional changes in CV-STM are constrained compared to MC1 because of the assumption built into CV-STM that established trees will remain on the landscape until something removes them. Without disturbance, climate change had little effect on vegetation composition in CV-STM. The long-lifespans of many of the tree species (e.g., > 500 years for Douglas-fir) helps to justify this assumption. Higher levels of disturbance increased the convergence between predictions from CV-STM and MC1 because disturbance allowed IDUs in the study area to undergo more rapid successional changes as informed by MC1. If climate change is severe enough to directly kill dominant tree species, then the lag in CV-STM due to the need for stand-replacing disturbances would lead to erroneous results; we consider this unlikely, however, given the current mild climate of the study area and broad regional distribution of all of our dominant and subdominant tree species. The interaction between disturbance and climate change would be even stronger if changes in climate increased dominant tree species' susceptibilities to disturbance, e.g., from insect or pathogen outbreaks. The result of this

enhanced interaction would be to make the results of MC1 and CV-STM more comparable in the short-term.

To some extent, the minor effects of changing climate on vegetation change in CV-STM without disturbance is at odds with observations in other locations. Many studies have documented recent range shifts in plants without disturbance, sometimes contrary to the general expectation of species moving poleward or to higher elevations (Crimmins et al., 2011). Studies have suggested, however, that Douglas-fir may continue to dominate in the western Pacific Northwest under future climate change (Dale and Franklin, 1989; Busing et al., 2007), while the former study also concluded that climate-induced changes in disturbance regimes such as wildfire and insect outbreaks could be the primary cause of climate-driven vegetation change.

The implementation of disturbance in the model was spatially random and at regular intervals. This enabled us to more clearly test the effects of disturbance on model dynamics. The timing of vegetation changes projected by MC1 has the potential to substantially alter successional trajectories in the model when a mechanistic fire model and tree harvest are coupled with CV-STM in Envision. For example, under the Hadley projections with MC1 there were two periods of climate that were suitable for continental evergreen needleleaf forest growth (Figure 4.7). If a stand-replacing fire of large spatial extent were to occur during one of these periods, the resulting successional trajectories could increase the area ponderosa pine communities occupy; these changes could last for decades. Although MC1's projections of the future period with fire turned on did not include any fires during these periods, future simulations using FlamMap could project wildfires during these critical time periods, particularly since wildfires in the Willamette Valley are principally caused by human ignitions (Sheehan, 2011).

Some areas of any landscape are more or less suitable for habitat conservation, regardless of climate change. There are IDUs within our study area that remain or become open oak habitat; their fate depends on both disturbance and climate change (Figure 4.8). This modeled outcome agrees with the natural history of open oak habitats in the Willamette Valley. For much of the study area, however, under minimal climate change, many IDUs are far more likely to support Douglas-fir or bigleaf maple, depending on the disturbance regime. If climate change is more severe, these same IDUs

are likely to preferentially support Douglas-fir or madrone, again depending on the disturbance regime. Thus, our model identified important spatial constraints on conservation opportunities for oak savanna.

One of the major technical challenges in coupling different classes of models is bringing outputs and inputs from various models and data sources into congruence. We were able to downscale information from the 800-m grid cells in MC1 to smaller, irregular polygons in our study area by using soils data as descriptors of current potential plant growth in FVS. For this project, we also resolved contradictory descriptions of current vegetation from data sources that used different geographic representations of the landscape. We developed ways to match broad descriptions of potential vegetation types from a DGVM to plant communities of known species composition. We significantly correlated a metric of productivity from a global model of vegetation with one based on empirical measurements. Through all these steps we were able to train and constrain an STM that was parameterized from a biometric forest stand model of vegetation change to the vegetation responses to climate change projected under a DGVM.

Other modeling efforts that include detailed descriptions of vegetation, human land management, and disturbance are underway (Keane et al., 1996; Bachelet et al., 2001; Medvigy et al., 2009; Crookston et al., 2010). The approach we took with CV-STM yields a unique model that demonstrates complex behavior. CV-STM meets one of our key research goals: it contributes to climate-sensitive land-use and land-management planning. CV-STM will allow us to explore how changes in climate, human population, and land use policy may interact to affect wildland fire and ecological succession.

Conclusions

We have described the development of a new vegetation model, CV-STM, which projects spatially explicit successional trajectories based on individual tree dynamics, disturbance, and climate change at the local scale and fine grain at which land management decisions are made. To do so, we unified data sources that describe vegetation in fundamentally different ways and at different spatial resolutions. Our work demonstrates one way to provide local, fine-grained projections of vegetation change in future climates that are based on a mechanistic understanding of the physiological and

biogeochemical bases of plant community composition and growth.

By using output from a DGVM to adjust and constrain transition probabilities within an STM, we were able to provide estimates of successional trajectories that were markedly different from those generated by the DGVM. Based on current and historical successional dynamics in the study area, the assumptions underlying the vegetation modeling appear to be ecologically defensible. These differences between CV-STM and MC1 are apparent in the spatial and temporal dynamics of the models.

Our work demonstrates one way that DGVMs may substantially overestimate the rates of successional change in forests composed of long-lived trees in a human-dominated landscape under changing climate. Incorporating constraints on the successional changes from one forest type to another projected by a DGVM results in substantially different outcomes over a 90-year timeframe. Successional changes will also be closely tied to disturbance. The ability to accurately predict disturbance dynamics - including wildland fire, insects, pathogens, wind-throw, and harvest - will be central to the ability of any model to predict climate change effects on vegetation accurately.

Predicting the dynamics of disturbance will require the use of models that explicitly simulate human decision-making and the intrinsic lags in species' life cycles. CV-STM incorporates key dynamics of a DGVM, while addressing crucial limitations. These include not only basing future simulations upon the current vegetation and tempering the rates of successional change that occur, but also allowing human management to be incorporated mechanistically by modeling vegetation at a spatial grain and taxonomic resolution commensurate with the ways in which people manage the land. CV-STM is a central module within a larger modeling suite incorporated in Envision that will explore and document the interactions and feedbacks among climate change, ecological succession, wildland fire behavior, and human land-use decisions. Modeling tools such as this are among the many next steps that are necessary to develop effective, adaptive policies that can help our landscapes and societies adapt to rapidly changing climate.

CHAPTER V

CONCLUSIONS

“All models are wrong, but some are useful.” – *G. E. P. Box*

The application of climate-sensitive vegetation modeling to local land use decisions is a field that is still in its early development. In this dissertation, I have brought greater clarity to the dynamics of succession and disturbance for a critically imperiled ecosystem, and used this information to build a new climate-sensitive vegetation model for a landscape that includes this ecosystem. This research has advanced scientific understanding of tree growth rates and wildfire disturbance, and yielded technical and intellectual advances in vegetation modeling and climate change.

Summary of Major Results

- In areas of current and former Oregon white oak savanna in various stages of forest succession, there were significant site-specific differences in growth rates of the dominant tree species (Chapter II). This was true of both basal area growth increment and a radial growth increment that was standardized for tree age and size. These site-specific differences in tree growth rates correlated significantly with various measurements of plant competition, soils, and topography. However, these correlations were not consistently significant across sites for any species. I examined several different hypotheses for these weak and inconsistent environmental correlations with tree growth rates and concluded that these site-specific relationships are likely due to the complex land use, land management, and disturbance histories of the sites. Similarly complex controls on tree growth rates likely occur in many forests in the United States and elsewhere in the world.
- Forest cover types were strongly differentiated on the basis of plant community variables, but weakly differentiated on the basis of environmental variables (Chapter III). Individual fuel variables were significantly different among prairie, savanna, woodland, and forest cover types. Potential fire behavior, however, was significantly different for prairies and savanna cover types, but not for woodland and forest cover

types. The complex histories of land use, land management, and disturbance for the study plots likely contribute to this result.

- Classification and regression trees (CARTs) were more successful than descriptions of forest cover types at differentiating plots on the basis of fire behavior. CARTs relied on a variety of variables, but principally on topographic variables and non-linear combinations of plant community variables. This was true for both surface fires and crown fires, although simulations indicated that surface and crown fires were sensitive to different suites of variables. These results are especially important for land managers who seek to quickly prioritize stands for treatment to reduce fire hazard.
- Through collaboration with many colleagues, I was able to modify components of four existing modeling tools to build a new climate-sensitive vegetation state and transition model (CV-STM) (Chapter IV). Plant communities were defined by combinations of species composition, mean tree stem diameter, and canopy structure. Detailed changes in plant communities were then simulated based on coarse projections of vegetation changes from a large-scale, climate-sensitive vegetation model, MC1. CV-STM can therefore provide spatially-explicit information on local plant communities as climate changes in the future.
- CV-STM simulated successional dynamics with diverse and plausible spatial and temporal dynamics under a fully-crossed suite of climate change and disturbance scenarios. The rates of change in CV-STM were generally slower than in MC1; rates of change projected by CV-STM were also more plausible, based on historical observations of successional trajectories. CV-STM showed strong interactions between disturbance scenarios and climate scenarios, indicating that in landscapes where disturbance is governed by human decisions, the effects of climate change on successional trajectories will be strongly influenced by human activities.
- CV-STM is designed to be integrated with spatially-explicit and mechanistic models of human land-use decision making and fire. As part of a larger simulation modeling system, CV-STM will allow researchers, policy makers, and other stakeholders to explore approaches to land use and land management that may be more efficient and

economical for conserving and restoring critically imperiled ecosystems, and preserving ecosystem goods and services, under projected climate change.

Implications for Studying and Modeling Successional Dynamics

The complex interactions that result in ecological succession are the core of mechanistic projections of successional trajectories. Projections of successional trajectories are increasingly sought to understand the consequences of anthropogenic climate change and to develop adaptive strategies that can be used to alter the landscape in desired ways. My results indicate that the interplay between environmental variables and the legacies of land use and disturbance regimes can result in highly variable rates of tree growth and successional change. Tree growth over a single decade may not reflect the influences of variable climate and growth environment during a tree's lifespan, but the tree growth data in this dissertation are the most complete data set for the current and former Oregon white oak savanna habitats in the southern Willamette Valley. For various technical reasons, a more detailed, long-term growth record may never be available for these ecosystems. While more direct measurements of light and moisture availability might help predict individual tree growth rates, complex historical disturbances would likely still obscure landscape-wide patterns in individual tree growth rates, which were highly variable. Locations within a landscape that are similar in many regards may support rates of tree growth that are quite different, and therefore plant communities that are quite different as well.

Current vegetation is a stronger control over potential fire behavior than underlying environmental variables in current and former Oregon white oak savanna in the southern Willamette Valley. This is reasonable for landscapes with a history of extensive human land use and modification, given that current growth rates, and therefore current tree community composition, currently display only a weak, but complex relationship to underlying environmental variables. This contributes to my finding that, in landscapes undergoing diverse successional changes following a change in human land use and land management, traditional heuristics for predicting potential fire behavior work poorly. Many lands near human settlements – a large proportion of the environment with which humans interact on a daily basis – meet these criteria. At the very least, my

work indicates that more work is necessary to understand how potential fire behavior, and other types of disturbance, may affect lands near human settlements. Most previous work on fire behavior has been done in regions with a less complicated history of human disturbance. The contrast between previous work, and my research as presented in this dissertation, is therefore reasonable. For other locations with similar vegetation, climate, and land-use history, my work may help land managers directly identify targets for fuel reduction treatments.

Bearing in mind the complex interactions of environmental variables and land use history, the task of projecting changes in forest communities in conjunction with climate and human land-use changes may appear daunting. But my work has shown that it is possible to bring together classes of models and simulate changes in vegetation based on a mechanistic understanding of plant competition and succession. The projections of vegetation dynamics from this new model – CV-STM – are substantially different from other models’ projections. Like any model, CV-STM has its limitations. For example, the current parameterization of CV-STM includes no mechanistic representation of plant species dispersal, nor specific mechanisms of drought mortality. Nevertheless, CV-STM highlights the powerful effect that disturbance will have in shaping vegetation across the study landscape, whether that disturbance is fire, timber harvest, or something else entirely. Climate change effects on vegetation in the southern Willamette Valley will likely be large should they occur in concert with large or frequent disturbances, but much less dramatic in the absence of intense disturbances, due to the intrinsic inertia of existing communities. Because the model is spatially explicit, and has a fine spatial grain, it is able to identify areas of the landscape that may be especially dynamic or static under future climate and disturbance regimes. This information will benefit conservation and restoration efforts that are already underway, and may motivate new conservation and restoration projects.

What may be most exciting about this new model is how it will be used in the future. Current research efforts are already coupling this model with mechanistic models of fire behavior and effects, and human land-use decision-making. In that sense, CV-STM will provide land managers with a powerful, integrated tool for future decision-making. However, my approach to vegetation modeling should be relevant not only to land

managers who seek to answer similar questions in different regions, but also to researchers who wish to explore the interactions of succession, climate change, and land-use decision-making in general and provides a stepping-stone for future enhancements. The expansion of integrative modeling approaches over the coming years will be central to finding innovative adaptations to climate change.

APPENDIX

SUPPLEMENTAL MATERIALS TO CHAPTER IV

S1. CO₂ Parameterization Experiments

We attempted to explore the CO₂ parameterization in MC1 in two ways. The first way was to alter the atmospheric CO₂ concentrations that are input into the model. The idea was to use the actual A2 CO₂ concentrations as the “high” CO₂ fertilization effect, use a reduced CO₂ concentration ramp as the “low” CO₂ fertilization effect, and use a constant level of CO₂ (the recorded, 2006 level) as the “no” CO₂ fertilization effect. We found no difference in any MC1 output variables, except for the amount of C4 grass leaf area index, which increased by about 10% over the future period under the “high” CO₂ scenario.

The above approach is not ideal, since it changes the atmospheric concentration of CO₂ to achieve a physiological effect. The second way that we explored the CO₂ fertilization effect in MC1 was by changing the parameters, *co2itr* and *co2ipr*, that control the efficiency of plant respiration and photosynthesis. *co2itr* is the effect of doubling CO₂ concentration on the rate of transpiration, and *co2ipr* is the effect of doubling CO₂ concentration on the rate of photosynthesis. We equilibrated and ran the model under three different parameterizations of *co2itr* and *co2ipr* (Table S1). In 2007 (the first year of the model’s future run), the different CO₂ fertilization scenarios had no effect on the amount of live tree carbon (Table S2), tree net primary productivity (Figure S1), leaf shape index (Figure S2), and C4 grass leaf area index (Figure S3).

Table S1

Parameterization of *co2itr* and *co2ipr* to achieve different levels of CO₂ fertilization in MC1.

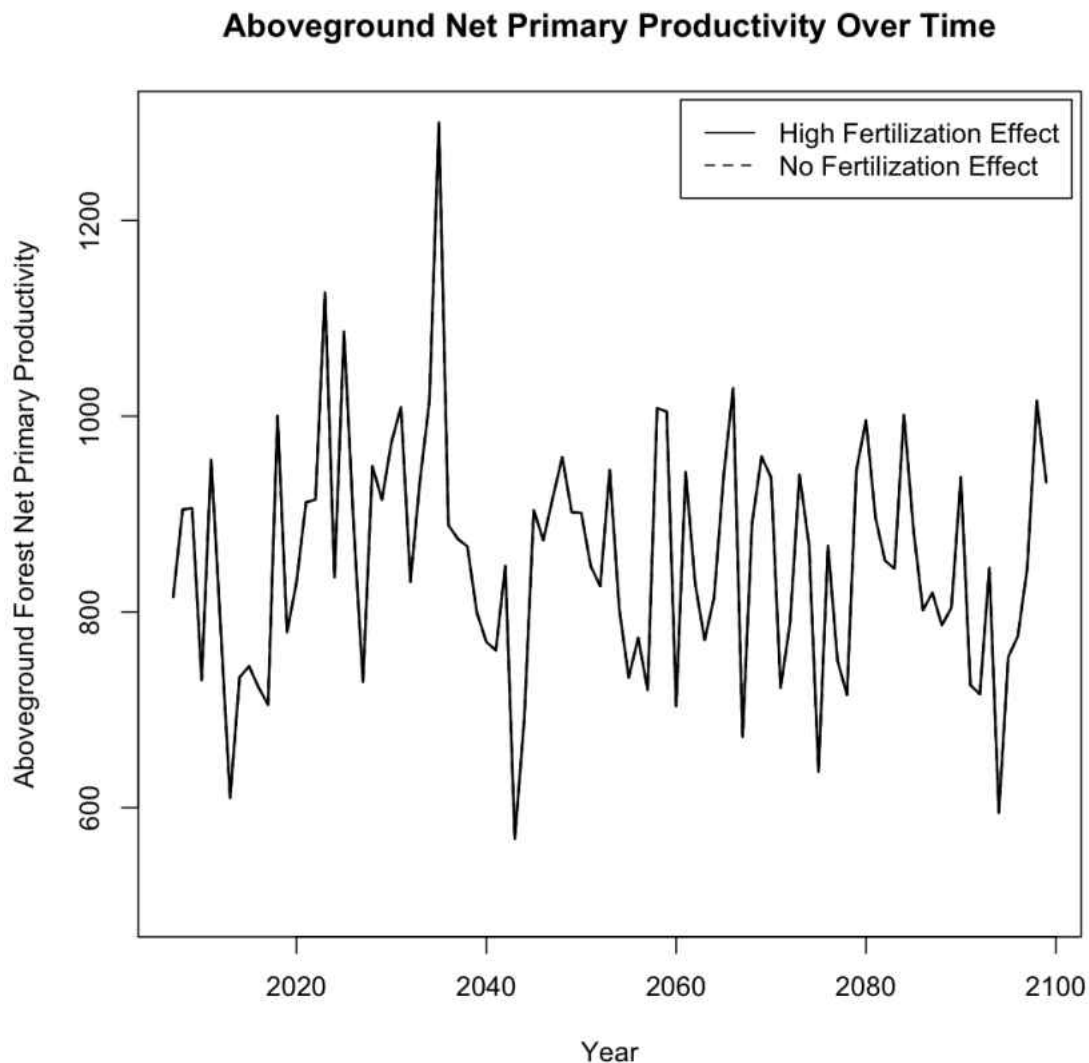
<i>CO₂ Effect</i>	<i>co2itr</i>	<i>co2ipr</i>
High	0.4	1.6
Moderate	0.75	1.25
None	1	1

Table S2.

Live tree carbon (kg/m^2) from three points in the study area in 2007.

Grid Cell	High CO ₂ Effect	Moderate CO ₂ Effect	No CO ₂ Effect
1	18.5	18.5	18.5
2	22.25	22.25	22.25
3	28	28	28

Figure S1. Aboveground tree NPP (g C/m^2) with no CO₂ fertilization effect, and with the high CO₂ fertilization effect, as specified in Table S1, for grid cell 2 from Table S2. Only one line is visible for this grid cell because the values were identical for the two simulations. All other grid cells examined show identical congruence between no and



high CO₂ fertilization simulations.

S2. STM Cover Type Descriptions

OA: Open broadleaf deciduous communities of drought-tolerant species, typically oaks.

May include other related genera, but must have canopy cover below 25%. This group includes most prairie and savanna.

OW: Broadleaf deciduous woodland of principally drought-tolerant species, typically oaks. May include other related genera. Must have canopy cover between 25% and 60%.

OD: Woodlands of drought-tolerant trees, dominated by broadleaf deciduous trees rather than needleleaf evergreen trees. Trees must have quadratic mean diameter (QMD) of at least 25.4 cm. If the QMD is less than 25.4 cm, these communities are usually described as *DO*.

DO: Woodlands and low-density forests of needleleaf evergreen trees growing above drought-tolerant broadleaf deciduous trees.

DD: Less mesic needleleaf evergreen woodlands and forests. These may contain a wide variety of species, but Douglas-fir typically dominates.

BM: Mesic broadleaf deciduous forest, bigleaf maple usually dominates in upland locations but may include species of alder, cottonwood and ash in riparian zones. This may include a substantial component of mesic needleleaf evergreen trees.

DM: Mesic mixed needleleaf evergreen and broadleaf deciduous forest. The typical needleleaf evergreen species is Douglas-fir, but there may be a grand fir component. The typical broadleaf deciduous species is bigleaf maple. The needleleaf evergreen component must be dominant over the broadleaf deciduous component.

DG: Mesic needleleaf evergreen forest. Douglas-fir is the dominant species, with grand fir as the subdominant species. There may also be substantial quantities of bigleaf maple.

M: Systems dominated by evergreen broadleaf species, typified by madrone. This must not include a substantial Douglas-fir component.

MD: Systems dominated by evergreen broadleaf species, with a substantial component of Douglas-fir .

P: Systems dominated by xeric evergreen species, typified by ponderosa pine. This

includes prairie, savanna and woodland systems.

The ctss (cover type, structural stage) description of an STM state is a concatenation of five components.

First is the cover type:

oa	Open deciduous oak habitat
ow	Deciduous oak woodland
od	Deciduous oak over Douglas-fir
do	Douglas-fir over oak
dd	Less mesic Douglas-fir
bm	Bigleaf maple
dm	More mesic Douglas-fir
dg	Douglas-fir and grand fir
m	Madrone
md	Mixed madrone and Douglas-fir
p	Ponderosa pine

Next is size class:

gfp	Grass-forb, post-disturbance
gf	Grass-forb
y	young (< 12.7 cm diameter-at-breast-height [dbh])
p	pole (12.7 – 25.4 cm dbh)
s	small (> 25.4 – 50.8 cm dbh)
l	large (> 50.8 cm dbh)

Canopy closure is next, although it is only included for size classes p, s and l:

o	Open canopy (<25% canopy cover)
m	Medium closure (25 – 60% canopy cover)
c	Closed canopy (>60% canopy cover)

An exception to this rule is the dd cover type, for which open is defined as $\leq 60\%$ canopy

cover, and medium canopy closure is $> 60\%$ canopy cover.

Next is the canopy layering, included only for sizes s and m :

- 1 Single canopy layer
- 2 More than one canopy layer

Finally, there may be “rf” appended, indicating a managed state with reduced fuels, or a “p” indicating a post-disturbance state that persists for only a single year to allow PVT affects on stand regeneration to be implemented. In its current implementation, the STM in CV-STM includes a total of 111 unique states, although the current design could support up to 396 states.

S3. R Code to Run CV-STM Outside of Envision

```
#####  
#  
# Author: Cody Evers  
# Edited by : Gabriel Yospin  
# Last revision date: 10.13.2011 0920 HRS PST  
#  
# This file will run simulations of probabilistic vegetation changes  
# and then plot them. The number of simulations, years to simulate, and  
# the parameters for the vegetation model are all user-specified.  
#  
# TODO: Turn this into a simple function!  
#  
#####  
  
# Choose the appropriate directory  
setwd("/Users/gyospin/Dropbox/Current Projects/Dissertation/Modeling/My  
Writing/Figures/Napoleon Figures/")#Work  
setwd("/Users/Gabriel/Dropbox/Current Projects/Dissertation/Modeling/My  
Writing/Figures/Napoleon Figures/")#Home  
  
# Read in the necessary files  
STM_master = read.csv("MC1_probability_transition_lookup.csv")
```

```

CTSS_aux = read.csv("ctss-output.csv", row.names=1)
# Modify the ctss lookup to create a more condensed plot
CTSS_aux$yvalue = c(1:58)

# Specify the values of parameters for the model run
STM_sub = subset(STM_master, conserve == 0
                 & si == 100
                 & pvt == 6
                 & regen == 1)
STM_sub = STM_sub[,c("vegclass1", "vegclass2", "p")]
startState = 243 # Use 203 or 243
numRuns = 100
numYears = 500
list = c(1:(numRuns * numYears))
df = data.frame(matrix(list, nrow=numRuns, ncol=numYears))
colnames(df) = c(1:numYears)
df = df * NA
df[,1] = startState
for (i in c(1:numRuns)) {
  print(i)
  for (j in c(1:(numYears-1))) {
    veg1 = df[i,j]
    probTab = subset(STM_sub, vegclass1 == veg1)
    mlist = NA
    for (x in c(1:nrow(probTab))) {
      list = rep(probTab$vegclass2[x], probTab$p[x] *
10000)
      mlist = c(mlist, list)
    }
    mlist = mlist[2:length(mlist)]
    veg2 = sample(mlist, 1)
    df[i,j+1] = veg2
  }
}
# Replace the veg class values with a condensed list from the lookup
table
for (i in c(1:numYears)) {
  colData = data.frame(df[,i])

```

```

        colData = merge(colData, CTSS_aux, by.x = colnames(colData[1]),
by.y = "vegstate1", all.x = TRUE)
        df[,i] = colData$yvalue
    }
# Plot the results
plot(x = c(1,numYears), y = c(0,60), main = c("Successional
Trajectories for ",startState," Over Time"),
      xlab = "Time (years)", ylab = "Vegetation Class", xlim = c(0,600),
ylim = c(0,60), axes = FALSE, type="n")
# Color the background by veg type
rect(0, 0, 500, 6, border = NA,
col=rgb(250,250,0,50,maxColorValue=255))#Yellow OA
rect(0, 6, 500, 10, border = NA,
col=rgb(250,125,0,50,maxColorValue=255))#Orange OW
rect(0, 10, 500, 12, border = NA,
col=rgb(180,100,0,50,maxColorValue=255))#Dk Orange OD
rect(0, 12, 500, 18, border = NA,
col=rgb(140,250,0,50,maxColorValue=255))#Lt Green DO
rect(0, 18, 500, 27, border = NA,
col=rgb(60,100,0,50,maxColorValue=255))#Dk Green DD
rect(0, 27, 500, 34, border = NA,
col=rgb(50,175,130,50,maxColorValue=255))#Teal DM
rect(0, 34, 500, 36, border = NA,
col=rgb(50,100,100,50,maxColorValue=255))#Slate DG
rect(0, 36, 500, 41, border = NA,
col=rgb(0,250,250,50,maxColorValue=255))#Lt Blue BM
rect(0, 41, 500, 47, border = NA,
col=rgb(250,180,250,50,maxColorValue=255))#Lt Pink PS
rect(0, 47, 500, 50, border = NA,
col=rgb(80,10,60,50,maxColorValue=255))#Maroon PW
rect(0, 50, 500, 56, border = NA,
col=rgb(200,80,250,50,maxColorValue=255))#Pink M
rect(0, 56, 500, 59, border = NA,
col=rgb(200,0,100,50,maxColorValue=255))#Dk Pink MD
# Add an axis for time, with ticks every 100 years
axis(1, at = c(0,100,200,300,400,500), labels =
c("0","100","200","300","400","500"),
      pos = 0.025, tck = 0.908, col.ticks = "white")

```

```

#axis(2, lwd = 0, lwd.ticks = 1, col.ticks = "grey", at = c(1:59),
labels = NA, tck = 0.77, pos = 0.11)
## Add a legend
#leg.txt <-
c("MD", "M", "PW", "PS", "BM", "DG", "DM", "DD", "DO", "OD", "OW", "OA")
#legend("topright", legend = leg.txt, inset = 0, title = "Community
Types",
#       fill = c(rgb(200,0,100,50,maxColorValue=255),
rgb(200,80,250,50,maxColorValue=255),
#           rgb(80,10,60,50,maxColorValue=255),
rgb(250,180,250,50,maxColorValue=255),
#           rgb(0,250,250,50,maxColorValue=255),
rgb(50,100,100,50,maxColorValue=255),
#           rgb(50,175,130,50,maxColorValue=255),
rgb(60,100,0,50,maxColorValue=255),
#           rgb(140,250,0,50,maxColorValue=255),
rgb(180,100,0,50,maxColorValue=255),
#           rgb(250,125,0,50,maxColorValue=255),
rgb(250,250,0,50,maxColorValue=255)),
#       bty = "n")
# Add horizontal white lines
boxbounds = c(6,10,12,18,27,34,36,41,47,50,56)
for (i in c(1:length(boxbounds))) {
  abline(boxbounds[i], 0, col = "white", lwd = 3)
}

# Plot the data
for (z in c(1:nrow(df))) {
  x = 1:(numYears)
  y = as.double(df[z,])
  lines(x = x, y = jitter(y, factor = 1, amount = 0.4),
        col=rgb(0,0,0,10,maxColorValue=255),lwd=2)
}
# End

```

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