POSTGLACIAL TRANSIENT DYNAMICS OF OLYMPIC PENINSULA FORESTS:

COMPARING PREDICTIONS AND OBSERVATIONS

by

DAVID M. FISHER

A THESIS

Presented to the Department of Geography
and the Graduate School of the University of Oregon
in partial fulfillment of the requirements
for the degree of
Master of Science

June 2013

THESIS APPROVAL PAGE

Student: David M. Fisher

Title: Postglacial Transient Dynamics of Olympic Peninsula Forests: Comparing Predictions and Observations

This thesis has been accepted and approved in partial fulfillment of the requirements for the Master of Science degree in the Department of Geography by:

Daniel G. Gavin	Chairperson
Patrick J. Bartlein	Member

and

Kimberly Andrews Espy	Vice President for Research and Innovation; Dean of the Graduate School

Original approval signatures are on file with the University of Oregon Graduate School.

Degree awarded June 2013

THESIS ABSTRACT

David M. Fisher

Master of Science

Department of Geography

June 2013

Title: Postglacial Transient Dynamics of Olympic Peninsula Forests: Comparing Predictions and Observations

Interpreting particular climatic drivers of local and regional vegetation change from paleoecological records is complex. I explicitly simulated vegetation change from the late-Glacial period to the present on the Olympic Peninsula, WA and made formal comparisons to pollen records. A temporally continuous paleoclimate scenario drove the process-based vegetation model, LPJ-GUESS. Nine tree species and a grass type were parameterized, with special attention to species requirements for establishment as limited by snowpack. Simulations produced realistic present-day species composition in five forest zones and captured late-Glacial to late Holocene transitions in forest communities. Early Holocene fire-adapted communities were not simulated well by LPJ-GUESS. Scenarios with varying amounts of snow relative to rain showed the influence of snowpack on key bioclimatic variables and on species composition at a subalpine location. This study affirms the importance of exploring climate change with methods that consider species interactions, transient dynamics, and functional components of the climate.

CURRICULUM VITAE

NAME OF AUTHOR: David M. Fisher

GRADUATE AND UNDERGRADUATE SCHOOLS ATTENDED:

University of Oregon, Eugene
University of Rochester, Rochester, New York

DEGREES AWARDED:

Master of Science, Geography, 2013, University of Oregon
Bachelor of Arts, Environmental Studies, 2007, University of Rochester

AREAS OF SPECIAL INTEREST:

Paleoecology and Biogeography
Geographic Information Systems

PROFESSIONAL EXPERIENCE:

GIS Consultant, Social Sciences Instructional Lab, University of Oregon, 2012-2013

Graduate Teaching Fellow, Department of Geography, University of Oregon, 2010-2012

PUBLICATIONS:

Gavin, D. G., D. M. Fisher, E. M. Herring, A. White, and L. B. Brubaker. 2013. "Paleoenvironmental Change on the Olympic Peninsula, Washington: Forests and Climate from the Last Glaciation to the Present." Report on file at the Olympic National Park, Port Angeles, WA.

ACKNOWLEDGMENTS

My sincere thanks go to Dr. Jed Kaplan for his generous technical assistance and collaboration on this project. I thank Professor Dan Gavin for continuous support and encouragement. Thanks to Professor “Bart” Bartlein for expert counsel and for acquiring the climate data. I appreciate support from the National Park Service/Cooperative Ecosystem Study Unit (Grant J8W07100028) and from Dave Conca from Olympic National Park for aiding with obtaining funding. In addition, special thanks to all the lab technicians and field crews who toiled to make the paleoecological data available for projects like mine. I also thank the Department of Geography and the Social Sciences Instructional Lab at the University of Oregon for supporting me as a Graduate Teaching Fellow as I completed this project.

For Claire, whose hospitality and generosity are unmatched.

TABLE OF CONTENTS

Chapter Page

LIST OF FIGURES

Figure Page

LIST OF TABLES

Tables Page

CHAPTER I

INTRODUCTION

Climate is the most important determinant of plant species abundance and distribution across broad spatial and temporal scales (F. I. Woodward 1987). Over the past 14,000 years, dramatic changes in the seasonal cycle of incoming solar radiation, ice-sheet extent and greenhouse gas concentrations, have altered global climate, including temperature, snowpack, disturbance regimes and other facets of the climate to which plants directly respond (COHMAP Members 1988). In North America, local-to-continental-scale changes in plant communities, as recorded by detailed pollen records, are strongly associated with regional climate change (Prentice, Bartlein, and Webb III 1991; Shuman et al. 2004). However, interpreting the particular climatic drivers of vegetation change is very complex and, ideally, independent evidence of past climate should be compared to the reconstructed vegetation (Webb 1986). A promising avenue exists to formalize this comparison in the application of dynamic vegetation models to explicitly simulate vegetation from a given paleoclimatic scenario and compare the results to observed vegetation change (Miller et al. 2008). Accurately predicting future effects of climate change relies on our ability to correctly model the dynamics of the past.

In the maritime Pacific Northwest, vegetation change from the late-Glacial period to the present is well documented in the paleoecological record (Whitlock 1992; Walker and Pellatt 2008), but no study has yet attempted to model the dynamic postglacial vegetation changes in this region. The low-elevation Puget trough vegetation transitioned from tundra and open parkland to woodland and dry forest in the early Holocene and then to temperate conifer rainforest in the middle Holocene (Cwynar 1987; Whitlock 1992).

High elevations formerly occupied by alpine glaciers, with only grasses and herbs at their margins, became forested with subalpine tree species, though tree establishment in the highest-snow cover areas was delayed until the middle Holocene (Gavin et al. 2001). Snowpack plays a very important role in the elevational zonation of the dominant tree species and at the alpine treeline (Henderson et al. 1989; Ettinger, Ford, and HilleRisLambers 2011) For example, studies of present-day vegetation-climate relationships on the Olympic Peninsula, WA show that high elevation west side tree growth is negatively correlated with snowpack and northeastern rainshadow tree growth responds negatively to summer temperature and positively to summer precipitation (Nakawatase and Peterson 2006). For the mountains of the Pacific Northwest, ongoing climate change is likely to manifest in reduced snowpack and warmer summer and fall seasons (Salathé et al. 2010).

In this study, we utilized LPJ-GUESS, a transient, dynamic, vegetation model that couples biogeochemical interactions among soil, biosphere, and atmosphere with stand-scale gap dynamics (Smith, Prentice, and Sykes 2001). A process-based model such as this is ideally suited for understanding the coupled effects of climate, disturbance, and competition among species. We utilized this model, driven by a simulated climate derived from a transient simulation with an Atmosphere-Ocean General Circulation Model (AOGCM) (Liu et al. 2009), to explain the vegetation history captured in five radiocarbon-dated pollen records on the Olympic Peninsula. The five sites span steep elevation and precipitation gradients, and thus capture a spectrum of climate conditions such as growing season length and summer moisture availability, which are both mediated by snowpack. The model is parameterized using well-known relative rankings of species traits (e.g., shade tolerance). We paid particular attention to species establishment limited by snowpack persistence. In regions such as the Olympic Peninsula with deep spring snowpack, seedling and tree growth is limited by the duration of spring snowpack, providing a major control of elevational distribution of species (Ettinger, Ford, and HilleRisLambers 2011).

This analysis provides a unique examination of the species-climate relationship in Pacific Northwest forests in that (1) 14,000 years of simulated climate data are used to drive a mechanistic transient vegetation model, (2) the simulated vegetation changes are validated by a temporally continuous comparison to paleoecological records, and (3) individual species are simulated as opposed to aggregated plant functional types (PFTs), thereby allowing species to respond individualistically to changing climate

CHAPTER II

METHODS

Study Area

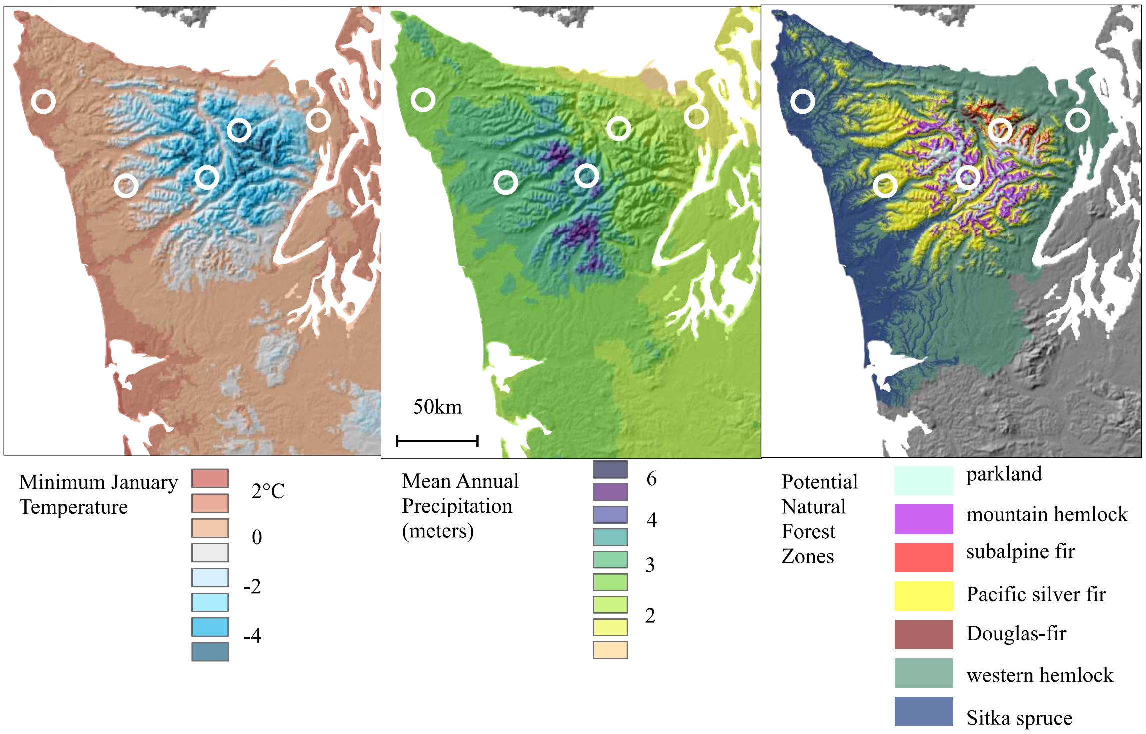
The Olympic Peninsula is a topographically complex and heavily forested region. Coastal plains of the southern and western peninsula rise to the Olympic Mountains (highest point 2430 m a.sl.) that have been shaped by a series of Pleistocene glaciations (Thackray 2001). The mountainous terrain and predominantly southwesterly onshore flow create a very steep precipitation gradient across the peninsula (Figure 1). The west coast receives over 2500 mm of annual precipitation and the western slopes at high elevation can receive over 5000 mm. In the rainshadow (northeastern) part of the region, mean annual precipitation is ca. 2000 mm at high elevations and drops to less than 500 mm on the northeast coast. The majority of precipitation occurs in the winter months, but snow is rare below 800 m elevation. Glaciers persist at the highest elevations in the interior of the peninsula.

Five lake-sediment records on the Olympic Peninsula, dating from the end of the Fraser Glaciation (less than 15 ka) to present, have been previously analyzed for pollen, macrofossils, and charcoal (McLachlan and Brubaker 1995; Gavin et al. 2001; Gavin, Brubaker, and Greenwald 2013; Gavin et al. 2013). These sites span the range of forest types and reflect the spatial heterogeneity of the topography and climate on the Peninsula (Figure 1; Table 1; (Henderson et al. 2011)). We refer to each site with respect to its elevation (low, middle or high) and occurrence in the windward (west) or rainshadow (east) portion of the peninsula. The low-west site (Wentworth Lake) is a 14 ha kettle lake located in the Sitka Spruce Zone. This zone occurs along the Pacific coast and extends inland along wide glacially-carved valleys, and supports some of the most productive and massive forests in the conterminous United States (Kellndorfer et al. 2010). The low-east site, (Crocker Lake) is a 26 ha lake in a glacial-outwash basin in the Western Hemlock Zone. This zone is the most widespread zone, covering areas north, south, and east of the Olympic Mountains, and valley slopes to the west. The middle-west site (Yahoo Lake) is a 4 ha cirque lake situated on a ridgetop at the transition between the Western Hemlock and the Pacific Silver Fir Zone, which is marked by a transition to montane forests and increasing snowpack The high-west site (Martins Lake) is a 1 ha basin on a ridge in the Mountain Hemlock Zone. This zone comprises the highest-elevation continuous forest and parkland of the west and central Olympic Mountains. The high-east site (Moose Lake) is a cirque lake in the Subalpine Fir Zone. This zone comparises the highest-elevation forest and parkland in the rainshadowed northeastern Olympic Mountains. Two additional zones exist on the peninsula that are not represented by a pollen record. A spatially restricted Douglas-fir Zone occurs at low-mid elevations in the driest locations of the northeast Olympic Mountains, and the Subalpine Parkland Zone marked by meadows and tree clumps occurs at the highest elevations. Whereas this forest zonation is well established (Fonda and Bliss 1969), individuals of any species may be found on certain microsites outside of their zone of dominance. The environmental and ecological factors controlling tree species distributions continue to be explored (Peterson, Schreiner, and Buckingham 1997; Nakawatase and Peterson 2006; Henderson et al. 2011).

Table 1. Study site characteristics. MASL – meters above sea level; MAP – mean annual precipitation (Wang et al. 2012); Soil Class – description of LPJ-GUESS soil code transferred from USDA soil textural codes following Prentice et al. (1992).

Site name	Lon (ºE)	Lat (ºN)	MASL (m)	MAP (mm)	Primary climax species	Seral Tree Species	Soil Class
Wentworth Lake (low-west)	-124.53	48.01	47	2779	Sitka spruce, western hemlock, western redcedar	Douglas-fir, red alder	Medium-Coarse
Yahoo Lake (mid-west)	-124.02	47.68	717	3657	Pacific silver fir, western hemlock, western redcedar	Douglas-fir, red alder	Medium
Martins Lake (high-west)	-123.53	47.71	1423	4812	mountain hemlock, Pacific silver fir	slide alder, mountain hemlock	Medium
Moose Lake (high-east)	-123.35	47.88	1544	2361	subalpine fir	subalpine fir, lodgepole pine	Medium
Crocker Lake (low-east)	-122.88	47.94	54	859	western hemlock, western redcedar	Douglas-fir, red alder	Fine

Figure 1. Environmental gradients of the Olympic Peninsula, WA. Minimum January Temperature and Mean Annual Precipitation from PRISM (Daly et al. 2008); Potential Natural Forest Zones (Henderson et al. 2011). White circles represent study sites.



Model Description

We used LPJ-GUESS, a dynamic vegetation model, to simulate the transient dynamics of post-glacial forests on the Olympic Peninsula. In LPJ-GUESS physiological processes such as carbon and water fluxes as well as interactions between soil, biosphere, and atmosphere are taken from LPJ-DGVM (Sitch et al. 2003) and stand dynamics of establishment and mortality are based on FORSKA, a forest gap model (Leemans and Prentice 1989; Prentice, Sykes, and Cramer 1993). Several studies have utilized LPJ-GUESS to understand the local and regional responses of vegetation to climate change and to explore ecosystem dynamics (Hickler et al. 2004; Miller et al. 2008; Tang, Beckage, and Smith 2012). These studies conclude that LPJ-GUESS is suitable for simulating species-level responses to climate and disturbance regimes.

LPJ-GUESS simulates the growth of cohorts of user-defined species or PFTs on a homogeneous patch of land. The patch size, 15 m x 15 m, approximates the area of influence of one mature tree (Zolbrod and Peterson 1999). Establishment of a given species on a patch is controlled by bioclimatic limits related to temperature, growing season length and intensity, and moisture availability (Table 2). When climate allows establishment of a species, probability of establishment is based on the shade tolerance of the species. Then, growth occurs annually when net primary productivity is allocated to leaves, sapwood, and roots based on a set of allometric relationships. Growth is limited by competition over light and moisture (Smith, Prentice, and Sykes 2001; Sitch et al. 2003). For example, shade-intolerant species establish with greater likelihood, but require more photosynthetically active radiation and higher growth rates to survive. Mortality is induced by stress (low-growth), disturbance, and maximum longevity.

Two types of disturbance exist in LPJ-GUESS. First, generic patch-clearing events occur with an annual probability equal to the inverse of a user-specified mean interval (750 years). Second, fire occurs probabilistically as a function of soil moisture and fuel availability. Therefore, the fire regime is dynamic, varying through time with climate and vegetation. This is particularly critical for modeling lowland temperate rainforest zones, where fire regimes varied over the Holocene in response to large-scale climate changes (Cwynar 1987; Brown and Hebda 2002). Fire behavior is not modeled in LPJ-GUESS, but a fire-resistance parameter assigned to each species defines the probability of survival (Table 2). Because many processes in the model are stochastic (e.g., disturbance, establishment, mortality) and that the patch size is fairly small, 30 replicate patches were simulated and annual output of carbon biomass was averaged.

Table 2. Species-level parameter values used in LPJ-GUESS. **Min TCM –** Minimum temperature of the coldest month for sapling establishment; **Max TCM –** Maximum temperature of the coldest month for saping establishment; **Min TWM –** Minimum temperature of the warmest month for sapling establishment; **PS-GDD$_5$ –** Post-snow growing degree-days above 5°C for sapling establishment; **fAWC –** fraction available water content of the soil to calculate water uptake and to limit sapling establishment; **k_latosa –** leaf-area to sapwood-area ratio used in allometric equations; **SLA –** specific leaf area; **Fire Resist –** probability of surviving a fire; **Max age –** Maximum age allowed in simulation.

Species	**Shade Group †**	**Min TCM (ºC)***	**Max TCM (ºC)***	**Min TWM (ºC)***	**PS-GDD$_5$**	**fAWC †**	**k_latosa ‡**	**SLA (m^2/g C) §**	**Fire Resist**	**Max age**
lodgepole pine *Pinus contorta*	Very Intolerant	-29.3	7	7	300	0.15	3500	8.5	0.05	250
subalpine fir *Abies lasciocarpa*	Very Tolerant	-15	-1	7.2	300	0.5	5400	7.6	0.05	250
mountain hemlock *Tsuga mertensiana*	Very Tolerant	-15	4	7.5	300	0.68	1600	9.2	0.05	400
Pacific silver fir *Abies amabilis*	Very Tolerant	-12	4	7	800	0.7	5500	13.5	0.05	400
Douglas-fir *Pseudotsuga menziesii*	Intolerant	-16	15	7	800	0.2	4200	9	0.3	750
western hemlock *Tsuga heterophylla*	Very Tolerant	-11.1	8.5	11.3	1400	0.6	4000	21	0.05	400
western redcedar *Thuja plicata*	Tolerant	-14	8	7.5	1400	0.5	5000	10.6	0.1	1000
red alder *Alnus rubra*	Very Intolerant	-13	10	7.5	1400	0.5	4000	23	0.05	80
Sitka spruce *Picea sitchensis*	Tolerant	-10	8	7	1600	0.7	4500	15	0.05	500
grass					50	0.01		32.4		

* (Thompson, Anderson, and Bartlein 1999)
† (Niinemets and Valladares 2006)
‡ (Waring, Schroeder, and Oren 1982; Turner et al. 2000; Martínez-Vilalta, Sala, and Piñol 2004)
§ (Kershaw Jr and Maguire 1995; White et al. 2000; Mitchell 2001; Duursma et al. 2005; Townend 1995; Chan, Radosevich, and Grotta 2003)

PFTs and Parameterization

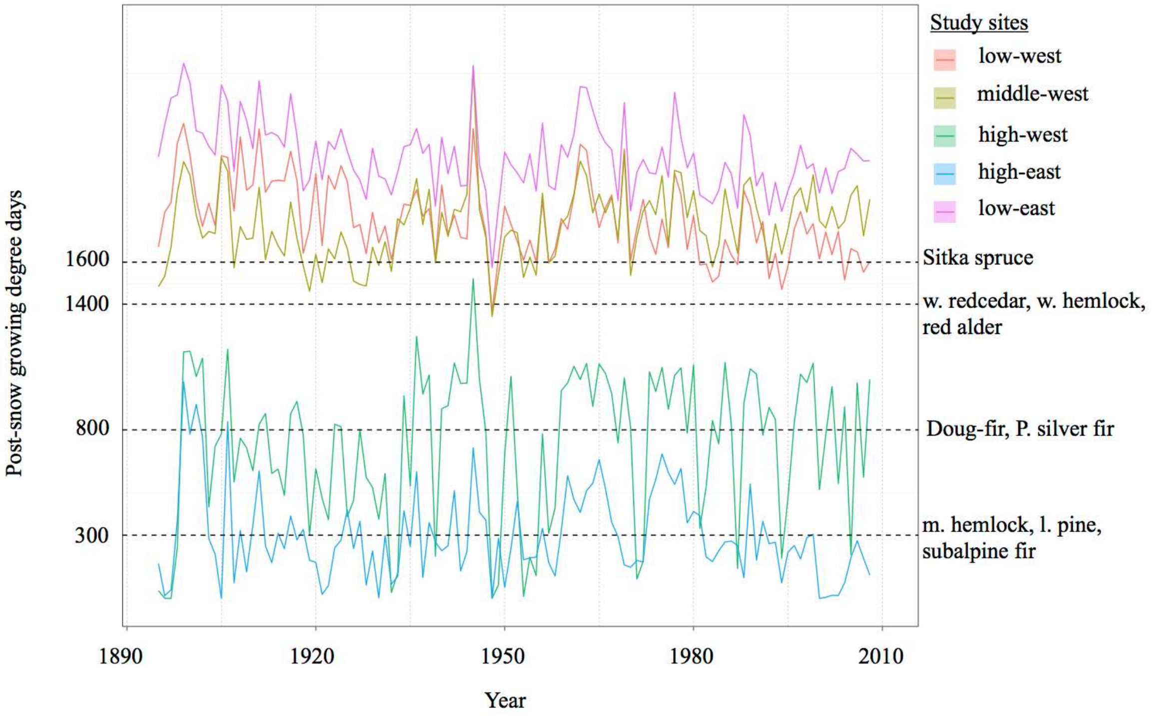
We defined and parameterized nine "plant functional types" to represent the common dominant tree species on the Olympic Peninsula and represented in pollen records. We defined an additional functional type to represent grass or meadow herbaceous species. Rare species and species associated with certain microsites (e.g. western white pine, yellow cedar and slide alder) were not included in these experiments because their occurrence is controlled by local factors including avalanche disturbances and topographic moisture (Franklin and Dyrness 1988), both of which are not represented in LPJ-GUESS.

We assigned species-specific bioclimatic and ecological parameters based on literature reviews (Table 2). We used four shade tolerance classes defined by Hickler (2004) and assigned species to them based on rankings in Niinemets and Valladares (2006). Fire resistance (probability to survive a fire) was based on bark thickness and observed survivorship in recent fires (Fischer and Bradley 1987; Agee 1996). Probability of surviving a fire was 30% for Douglas-fir, 10% for western redcedar, and 0.5% for all other species.

Our analyses of preliminary model output revealed a consistent dominance of low elevation species at mid and high elevation sites where they are absent today. This occurred because we intitally set the growing degree days above a 5°C base (GDD_5) as the threshold for establishment, with limits determined from the entire geographic range of the species as reported in Thompson et al. (1999). However, in regions of deep spring snowpack such as the Olympic Peninsula, the growing season experienced by seedlings is limited by the duration of spring snowpack, which provides a major control of elevational distribution of species. Therefore, it was necessary to customize LPJ-GUESS to take into account the role of deep snowpack on seedling establishment and persistence (Barbour et al. 1991). We made modifications so that growing degree-days (above 5°C) began to accumulate only after the modeled snowpack had melted to less than 10 mm snow-water equivalent (SWE). We term this new bioclimatic variable “post-snow growing degree-days above a 5°C base” (PS-GDD$_5$). Similarly, the fraction of the plant-available soil water-holding capacity (fAWC) during the growing season (Hickler et al. 2012) is averaged only over the period when PS-GDD$_5$ are accumulating. Because much snow occurs at temperatures near the rain-snow transition, modeling accumulating and melting snow realistically may be beyond the scope of the Haxeltine and Prentice (1996) and Gerten et al. (2004) hydrological models. We chose a rain-snow threshold surface air temperature of 1°C, which often occurs when cold upper-level air occurs above a warmer marine-influenced surface air (Nolin and Daly 2006).

Annual PS-GDD$_5$ requirements for establishment of the simulated species are not known by empirical study. Therefore it was necessary to calibrate this parameter. We calculated annual PS-GDD$_5$ values at each study site for every year from 1895 to 2008 using the daily weather generator in LPJ-GUESS with inputs of monthly temperature and precipitation from PRISM, interpolated to a 400 m resolution grid using the ClimateWNA tool (Wang et al. 2012). Then, annual PS-GDD$_5$ required for establishment were assigned to each species by calibrating towards modern species composition at each study site (Figure 2).

Figure 2. Post-snow growing degree days throughout 20th century calculated by the LPJ-GUESS daily weather generator. Dashed lines are species requirements for sapling establishment.



Moisture availability controls species establishment at dry sites on the peninsula (Soll 1994; A. Woodward, Schreiner, and Silsbee 1995). Therefore, we implement LPJ-GUESS with the optional drought-limited establishment, wherein species are allowed to establish if fAWC on a patch exceeds the fAWC species paramter value. For each species, this parameter was initially determined following the drought tolerance rankings in Niinemets and Valladares (2006). Using the calibration methods used for PS-GDD$_5$, we assigned final fAWC parameter values between zero and one. We confirmed the realism of the PS-GDD$_5$ and the fAWC parameterization in trial runs of LPJ-GUESS for the last 1000 years at each site.

Environmental Inputs

LPJ-GUESS is forced by three sets of climate variables: monthly means of temperature, precipitation, and percent sunshine, which is transformed from the cloudiness variable discussed below. These variables were synthesized with the following spatial and temporal characteristics in mind in order to provide: 1) a continuous monthly time-series that spans the length of the longest pollen record in the region, with 2) realistic interannual variability needed to elicit appropriate vegetation dynamics, and 3) variation among study sites based on the influence of topography.

Climate variables spanning the the last 22 ka were obtained from the TraCE-21 project (Liu et al. 2009; He 2010), which employed a synchronously coupled atmosphere-ocean general circulation model (AOGCM, NCAR-CCSM3) to simulate climatic variation over the past 22,000 years (i.e. from the Last Glacial Maximum to present). The available data from the transient simulation includes seasonal averages (three-month periods) at decadal time steps, from 22 ka to present. This dataset, by nature of its GCM origin, is global in extent and coarse in spatial resolution. One grid cell contains the entire study area of the Olympic Peninsula. Because we required climate data at a higher spatial and temporal resolution, we downscaled these data. First, seasonal and decadal values were interpolated to produce monthly and yearly values. Then, monthly anomalies with respect to a 1961-1990 base period were calculated. These monthly anomalies do not have realistic interannual variability, which is critical for simulating vegetation (Ni et al. 2006).

Realistic interannual variability was estimated from a monthly time series of 20th century climate from PRISM for temperature and precipitation (Daly et al. 2008) and from the 20th-century Reanalysis V2 for cloudiness (Compo et al. 2011). For each month and each variable, the 20th century time series was detrended using a locally-weighted regression (40-yr window width) (Prentice, Harrison, and Bartlein 2011). Then, anomalies with respect to a 1961-1990 base period were calculated. Thirty-year segments of the 20th century timeseries of (detrended) anomalies were randomly sampled and added to consecutive 30-year segments of the TraCE-21 anomalies. This procedure resulted in a 22 ka-to-present monthly timeseries of anomalies of average temperature, precipitation, and cloudiness, with interannual variability equivalent to that of the 20th century.

Finally, this composite of monthly anomalies was added to monthly long-term mean (1961-1990) values at each of the five sites. For temperature and precipitation, PRISM long-term means were interpolated to a 400 m resolution grid using the ClimateWNA tool (Wang et al. 2012). Long-term means for cloudiness were bilinearly interpolated from the Reanalysis V2 data. The final result is a unique climate series for each study site.

Along with climate data, atmospheric carbon dioxide concentration and soil characteristics are the other envrionmental inputs to LPJ-GUESS. Annual CO_2 concentration was estimated from a spline fit to ice-core records (Krumhardt and Kaplan 2010). Soil textural characteristics were acquired from the USDA Soil Survey Geographic Database (SSURGO, http://soils.usda.gov/survey/geography/SSURGO/) and were translated to LPJ-GUESS soil types following Prentice et al. (1992).

Simulation Protocol

LPJ-GUESS was run with 21 kyr-long transient simulations at each site. No additional spin-up period was prescribed, because interpretation of results at each site begins only at the start of the pollen record. To validate results, simulated biomass averaged over the most recent 1000 years was compared to canopy cover data from a broad network of ecological plots (http://ecoshare.info/2009/12/07/nw-washington-core-data downloaded July 2012) to check for appropriate species presence with respect to elevation and precipitation gradients. To validate paleo-simulations, each PFT’s percentage of the total carbon biomass at a site was compared to pollen percentages which were first transformed by an “R-value” (Davis 1963) derived from a modern pollen-vegetation comparison (Gavin et al. 2005). The R-value accounts for the fact that some species are more prolific pollen producers than others. The relative dominance of species at each site through time was qualitatively compared between the simulation and the pollen record.

To further explore the role of snowpack at the site with the greatest snow accumulation, we varied the rain-snow temperature threshold from -2°C to +2°C. We examined these scenarios of varying amounts of snow for effects on PS-GDD_5, fAWC, fire occurrence, and species composition.

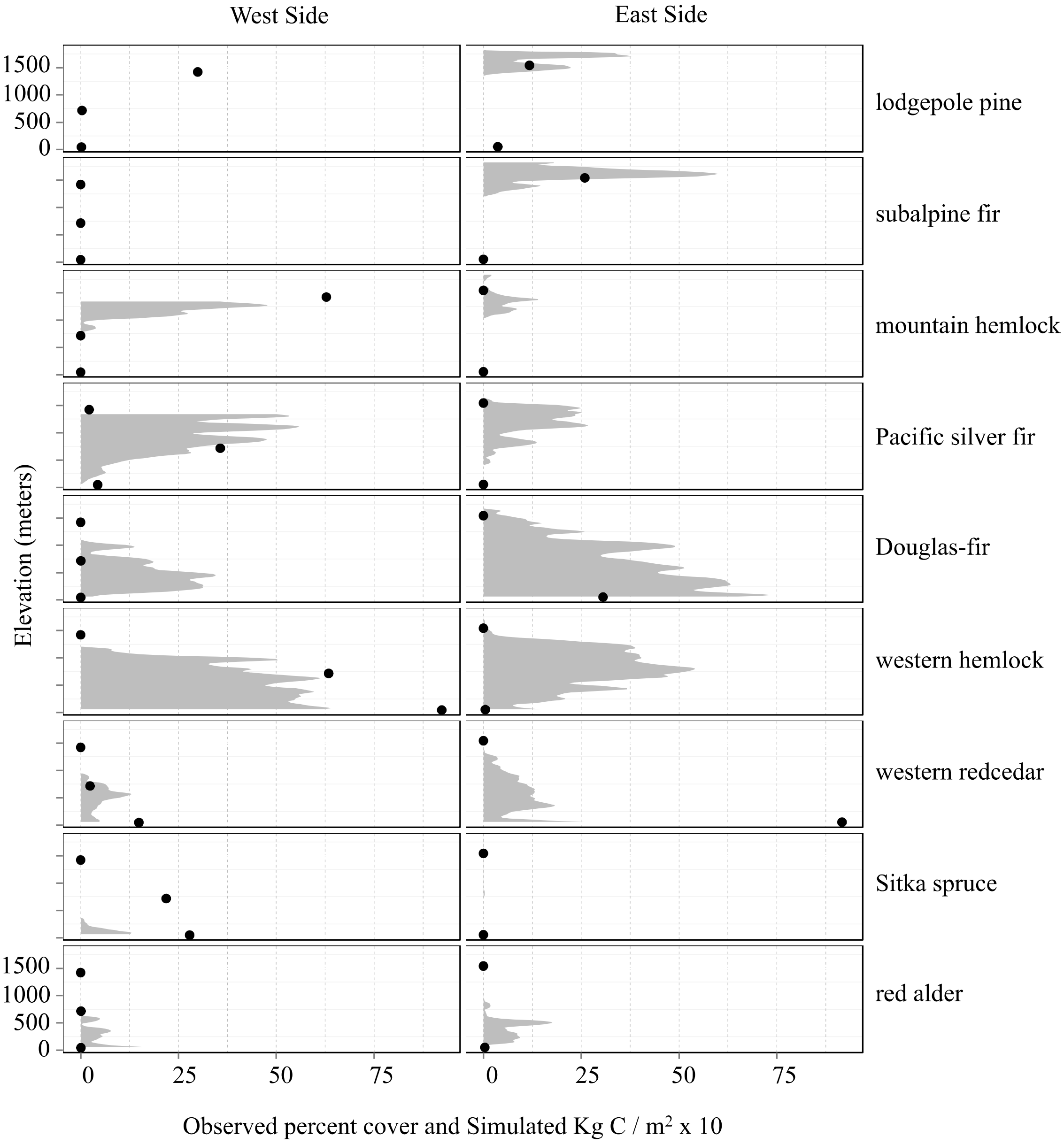
CHAPTER III

RESULTS

Present-day Elevational Distributions

LPJ-GUESS produced realistic present-day species composition with respect to elevation and precipitation gradients (Figure 3). On the western side of the peninsula, western hemlock is the most abundant species at low-to-mid-elevations but is absent at high elevations; this pattern was captured by the model at the three simulation sites in this region. Western redcedar and Sitka spruce are relatively minor components of the forest at low and middle elevations, a pattern captured by the model. Although Sitka spruce appears over-predicted by the model at the low-west site, this species is indeed abundant on the coastal plain near the low-west site, while the plot data in Figure 3 are biased towards the south and eastern flanks of the Olympic Mountains. Douglas-fir is common on lower south-facing slopes on the west side (Agee 1996), but it is correctly simulated as absent because neither the low-west or middle-west sites occurred in such locations. Pacific silver fir is a major component of the canopy at middle-to-high elevations and is simulated as abundant at the middle-west site, but as almost absent at the high-west site where this species reaches its upper elevational limit. Mountain hemlock is also correctly simulated at the high-west site, but lodgepole pine is also simulated as present, despite being absent in west-side montane forests.

Figure 3. Elevational distribution of present-day observed and simulated tree species. **Gray shading** – percent cover of tree species in 639 ecological plots in the Olympic National Forest (downloaded from Ecoshare.info); **Black dots** – simulated biomass of tree species averaged over the last 1000 years at each site and scaled by a factor of 10 in order to use the same scale as percent cover data. Plots and simulation sites are categorized as “west side” or “east side” with respect to the rainshadow.

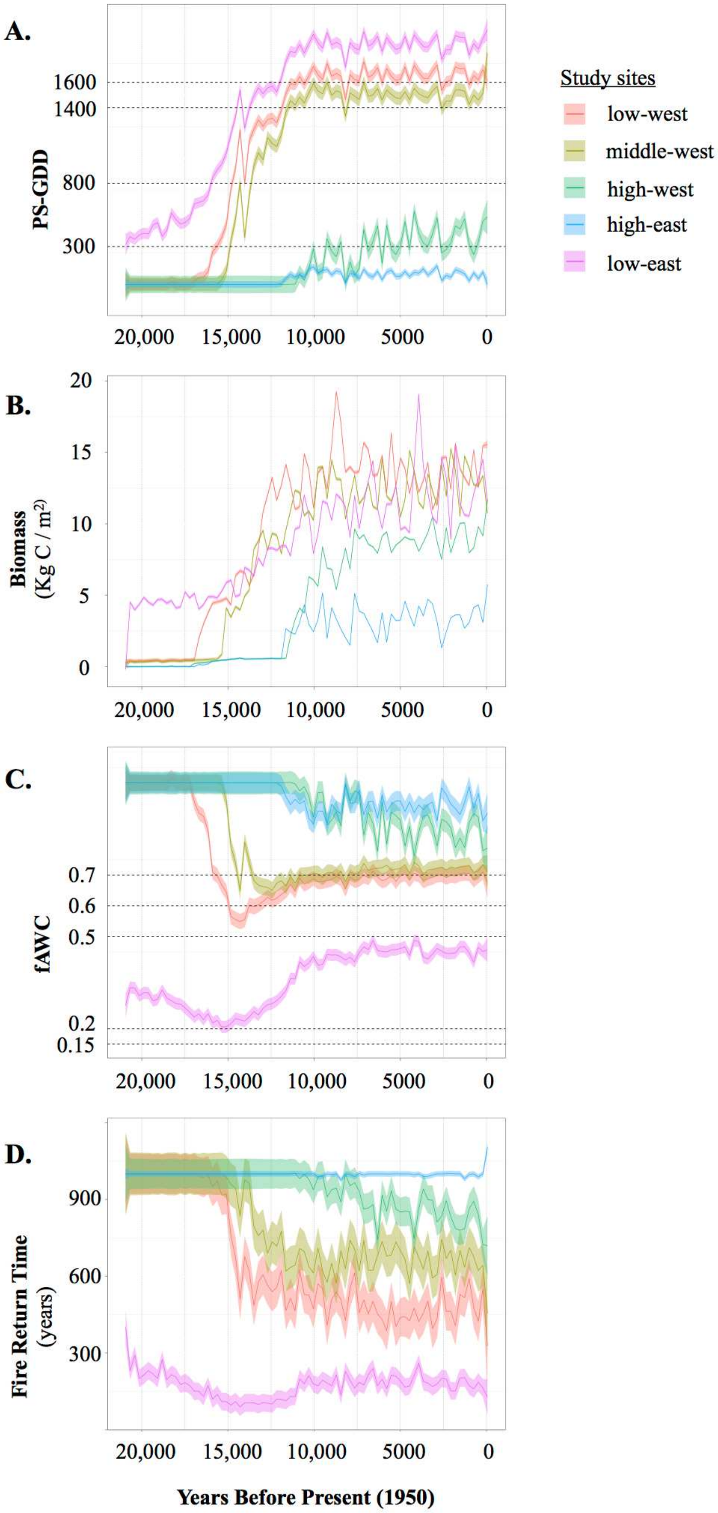


On the eastern peninsula, Douglas-fir and western redcedar are the most abundant species at low-to-middle-elevations, and their elevational distributions are generally matched by the simulation results. Western hemlock is common at middle elevations and correctly simulated as absent at the low-east site where it is rare and at the high-east site where it is absent. The highest east side elevations are dominated by subalpine fir with lodgepole pine as a secondary component, which is well matched by the simulation at the high-east site.

Late-Glacial to Present

The simulated biomass from 21 ka to present at each site closely follows the pattern of PS-GDD_5 (Figure 4). At the middle-west and high-elevation sites, the basal sediments pre-date the local arrival of trees. At these sites, simulated arrival of trees is marked by sharp increases in biomass that match the relative arrival times of trees inferred from pollen and other proxies (Gavin et al. 2001; Gavin, Brubaker, and Greenwald 2013). At the other sites, the sediment record begins with trees already present and the simulated biomass already increasing rapidly. Comparison of the fAWC variable across sites reveals that the low-east site is the driest and the high-elevation sites the wettest. Similarly, the low-east site also experiences the most frequent fire, with a return time less than 300 years, while simulated fire at the high-elevation sites is very rare (Figure 4).

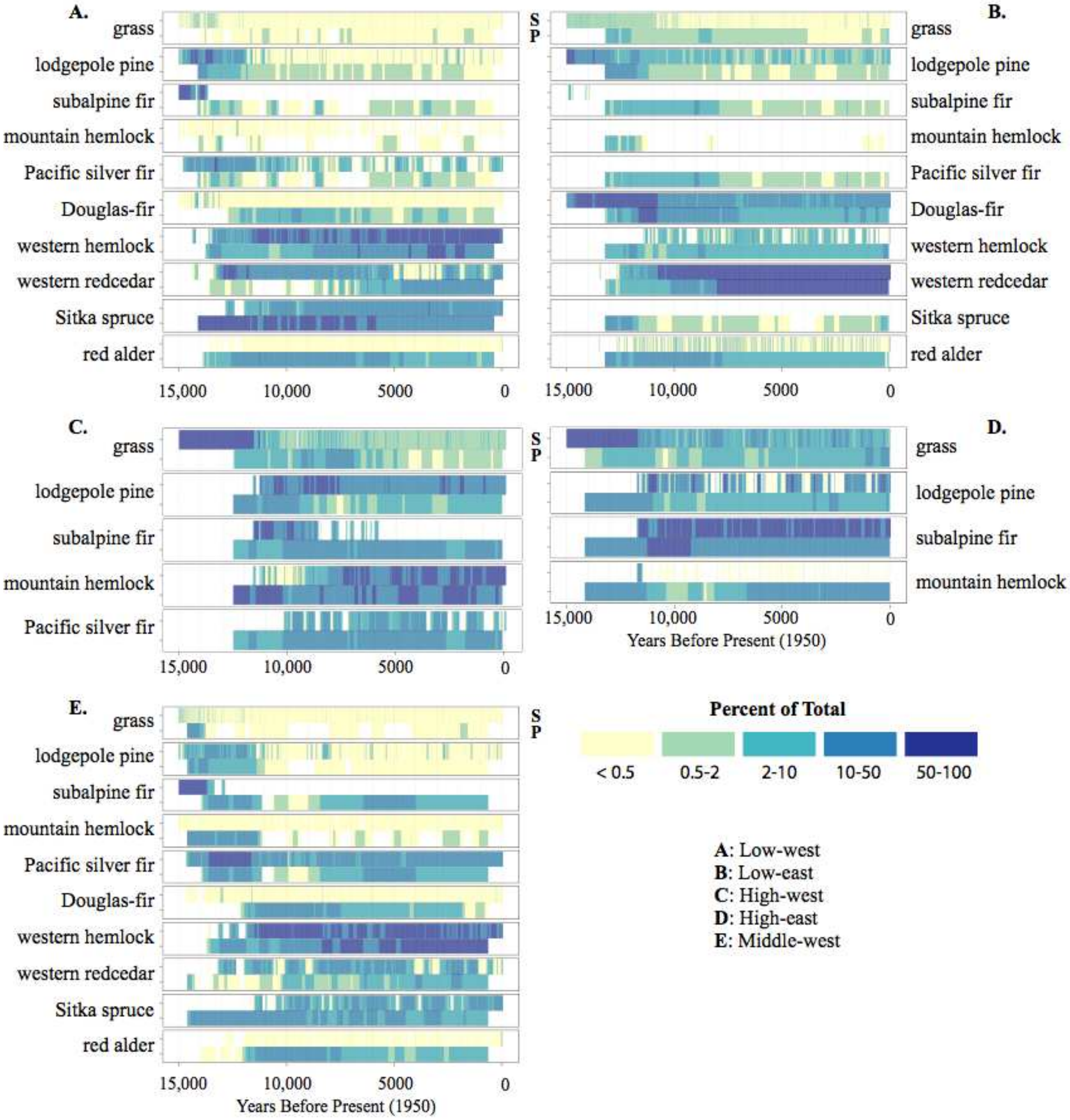
Figure 4. Site comparisons of LPJ-GUESS output from 21 ka to present. A) Post-snow growing degree-days above a 5°C base; dashed lines represent species requirement for establishment; B) Total simulated biomass; C) fraction available water content; dashed lines represent species requirement for establishment; D) Instantaneous fire return time.



Visual comparisons of simulations and pollen records (Figure 5) show that LPJ-GUESS generally simulated late-Glacial vegetation correctly, as well as the vegetation responses to the warming Holocene climate that are known from the paleoecological record at each site. The pollen record at the low-west site (Figure 5a) begins about 14 ka and shows a transition from lodgepole pine to red alder and Douglas-fir in the early Holocene, and to western redcedar, western hemlock, and Sitka spruce in the mid-late Holocene. LPJ-GUESS simulations at this site capture the late-Glacial and mid-late Holocene periods well, but fail to produce increased Douglas-fir and red alder during the early Holocene. Instead, the mesic late-successional species, which dominate the pollen record after about 9 ka, dominate the simulation starting around 13 ka. From that time to present, western redcedar, western hemlock, and Sitka spruce trade-off dominance in the simulated patches.

The pollen record at the middle-west site (Figure 5e) begins at 14.7 ka with lodgepole pine and mountain hemlock pollen appearing. Pacific silver fir, western hemlock and Sitka spruce pollen also appear in the late-Glacial but only achieve dominance after 8 ka. The early Holocene pollen record shows abundant red alder and Douglas-fir. Simulated biomass at this site shows a transition from lodgepole pine and subalpine-fir in the late-Glacial, to temperate shade-tolerant species taking over by 13 ka. Similar to the low-west site, Douglas-fir and red alder are underrepresented during the early Holocene compared to the pollen record. Pacific silver fir represents up to 10% of biomass between 14-11.5 ka, and only rarely reaches 10% after this period. Western hemlock and Sitka spruce alternate in dominance throughout the Holocene, with western redcedar rarely exceeding 10% of the biomass.

Figure 5. Simulated biomass (**S**) compared to pollen record (**P**). Subalpine fir and Pacific silver fir pollen are indistinguishable, thus their pollen records are identical when both are plotted. Species are only plotted if they are simulated present or interpreted as locally present in the pollen record.



The pollen record at the high-west site begins at 11.2 ka (Fig. 5c). Lodgepole pine, slide alder, and mountain hemlock pollen is most abundant, with trace amounts of other taxa. Alder pollen comprises more than 50% of the record from 10-8 ka. The decline in alder is complemented by relative increases in true fir (subalpine fir or Pacific silver fir), mountain hemlock, and western hemlock pollen. Macrofossils were identified in the lake sediment that represent all of these pollen types except western hemlock, pollen of which was likely regionally dispersed from low elevation. Simulations include abundant grass before 10 ka and from 9-8.5 ka and grass was otherwise present through the Holocene. Subalpine fir and lodgepole pine alternate dominance until 8.5 ka at which time mountain hemlock exceeds 50% of the biomass until present. Lodgepole pine is a consistently simulated present throughout the Holocene, along with occasional cohorts of Pacific silver fir and western redcedar.

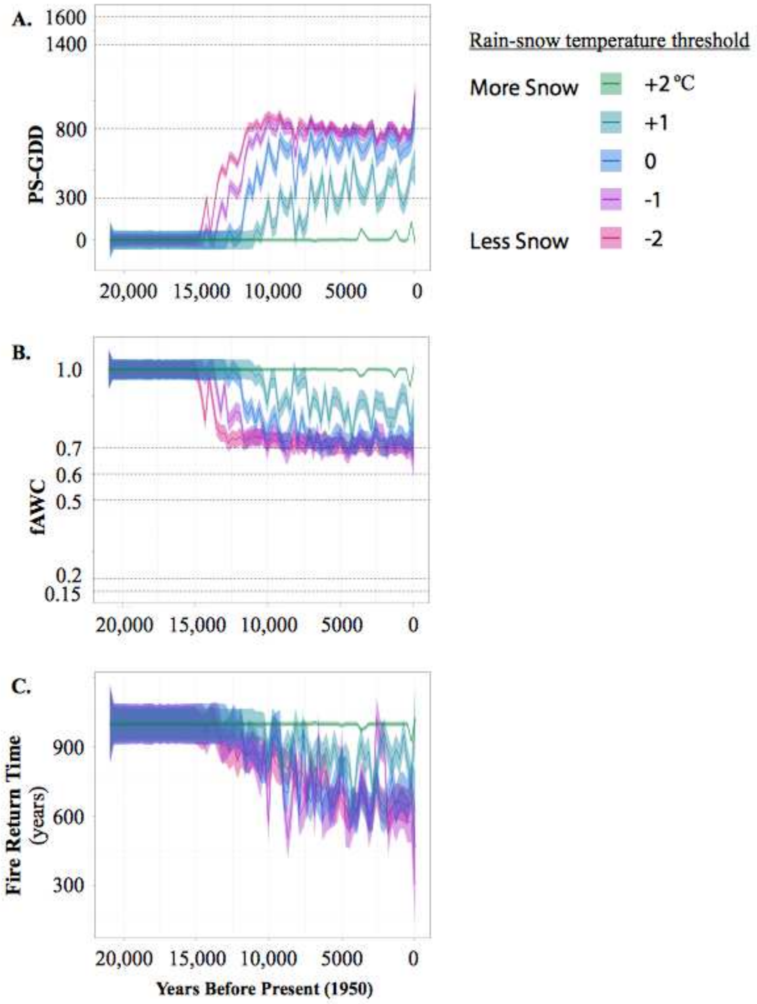
The high-east site pollen record shows relatively stable species composition from 14 ka to present (Figure 5d). Subalpine fir, lodgepole pine, and grass pollen are well represented, indicating that the subalpine fir and pine parkland that existed across much of the peninsula during the late-Glacial period has persisted until the present at this location. Simulation results are consistent with the pollen record; subalpine fir represents over 50% of the biomass at most times, with lodgepole pine as the second most abundant species. Grass is present throughout the simulation period, indicating some open canopy patches. Douglas-fir and mountain hemlock cohorts establish sporadically during the Holocene, but only rarely reach maturity

The pollen record at the low-east site begins about 13 ka, around the time of the regional decline in pine pollen that appears in all five records (Figure 5b). Grass, pine, and alder pollen types are the other main components of the pollen community in the late-Glacial. The early Holocene (11-9 ka) shows abundant Douglas-fir and red alder pollen, then by 8 ka the Cupressaceae pollen type dominates the record, with Douglas-fir and red alder remaining present along with western hemlock. LPJ-GUESS simulations begin with lodgepole pine and Douglas-fir as the dominant tree species, with grass present as well. The longer-lived Douglas-fir accounts for over 50% of simulated biomass until 10.5ka when western redcedar achieves dominance and maintains it throughout the Holocene. Douglas-fir remains present as the second most abundant species in good agreement with the pollen record. Simulated western hemlock does not appear until 11ka and its relative biomass only reaches between 10-50% of the simulated community a few times during the mid and late Holocene. Red alder is present at most times during the simulation period and represents a slightly greater component of simulated biomass between 11.5 and 8.5ka relative to other periods.

Effects of Snowpack on Bioclimatic Variables

Simulations with different rain-snow temperature thresholds at the high-west site reveal some important effects of the snowpack on PS-GDD_5, fAWC, and fire frequency (Figure 6). With a threshold temperature set at 2°C, snowpack almost always persists year-round, as indicated by the PS-GDD_5 curve rarely departing from 0. All three variables show greatest response to changes in the temperature threshold from 2°C to 0°C, and much less response to changes from 0°C to -2°C.

Figure 6. Five scenarios at the high-west site with varied rain-snow temperature thresholds and the response of A) Post-snow growing degree days above a 5°C base; dashed lines represent species' requirements for establishment; B) fraction available water content; dashed lines represent species' requirements for establishment; C) fire return time.



CHAPTER IV

DISCUSSION

LPJ GUESS is able to simulate realistic species composition at each study site, reflecting 1) the spatial pattern of forest types on the Olympic Peninsula and 2) major changes from the Late-Glacial to the Holocene. Important discrepancies between the pollen record and simulations occur mainly during the early Holocene, and possible explanations will be discussed.

Spatial Pattern of Forest Types

Results from this study corroborate conclusions drawn from earlier process-based and statistical model studies that explain climate-vegetation relationships in the PNW (Urban, Harmon, and Halpern 1993; A. Woodward, Schreiner, and Silsbee 1995; Zolbrod and Peterson 1999; Nakawatase and Peterson 2006; Littell et al. 2010). All of these studies support the broad theory that forests of western North America, examined at coarse spatial scales, are either limited by energy or by moisture (Stephenson 1998; Littell, Peterson, and Tjoelker 2008). Empirical studies of current species distributions across climatic gradients of the Peninsula and other PNW mountain ranges show that climate components related to growing season length and intensity are positively correlated with growth on windward slopes, and climate components related to summertime moisture availability are positively correlated with growth on leeward slopes (McKenzie et al. 2003; Nakawatase and Peterson 2006). From the Late-Glacial to the Holocene, simulated biomass at all sites follows the pattern of PS-GDD$_5$, suggesting that this variable is limiting total biomass. However, throughout the Holocene, the low-east site has consistently higher annual PS-GDD$_5$ sums than all other sites, but lower total biomass than the other two low-mid elevation sites. The low-east site also has much lower average fAWC and more frequent fires, suggesting moisture availability is limiting biomass at this low-elevation rainshadow site. (Figure 4).

In our customization of LPJ-GUESS, as in the real world, the bioclimatic variables PS-GDD_5 and fAWC are influenced by the duration of snowpack. The PNW receives most of its precipitation during the winter; January, December, and November are the three wettest months on the Olympic Peninsula. At high elevations this precipitation is often snow, but the maritime influence on the Peninsula keeps average surface air temperatures relatively high, near to the freezing point even in January. About sixty percent of the snow-covered area on the Olympic Peninsula has been deemed “at-risk” because minimal amounts of winter warming could convert much precipitation from snow to rain (Nolin and Daly 2006). The rain-snow temperature varies among precipitation events and there is no agreed upon mean value for the Olympic Peninsula. Observations at Blue Glacier in the 1950s determined +2°C was the right discriminant value (Rasmussen, Conway, and Hayes 2000) and developers of the LPJ water balance module use 0°C (Gerten et al. 2004).

With a change in the rain-snow threshold temperature from 1°C to 0°C, PS-GDD_5 at the high-west site increases enough to allow Pacific silver fir to be the dominant species instead of mountain hemlock. Mountain hemlock is found in mostly pure stands, or in stands mixed with Pacific silver fir at high elevations up to timberline on the western slope of the Olympic Mountains, such as at our high-west site. Initial simulations did not predict mountain hemlock at this site; it established along with Pacific silver fir and western hemlock but was outcompeted by these species because of their higher growth rates afforded by larger specific leaf area and leaf-area to sapwood-area ratio. Therefore, the key to mountain hemlock's success at this site and at similar locations in the PNW may be the exclusion of other species by persistent snowpack. Absolute temperature minima on the Olympic Peninsula do not drop below the tolerance of many of the simulated species (they are all present at much higher latitudes), but growing season length in temperate subalpine locations of the PNW is limited by snowpack as well as temperature. Thus, results suggest that mountain hemlock may have a substantially lower growing season requirement than other lower elevation mesic species, and that the PS-GDD_5 variable is an important one for predicting the distribution of tree species in subalpine environments.

Comparisons of Simulated Biomass to Pollen Records

Discrepancies between the pollen records and LPJ-GUESS simulations can be explained by 1) the poorly understood or highly variable relationships between biomass and pollen production, and the different spatial scales represented by the modeled and pollen-reconstructed forests, and 2) the inability of the GCM-derived input climate variables and the LPJ-GUESS solar insolation module to capture important variations since the Late-Glacial, most notably during the early Holocene.

Comparing biomass to pollen abundance is an uncertain and problematic process. First, pollen production is not proportional to biomass. We account for this by adjusting pollen percentages by factors derived from present-day relationships of surface pollen and percent canopy cover (Gavin et al. 2005). Second, pollen captured by these lakes is representative of the local and regional vegetation at the time, so taxa present in the pollen record may not be present in the forest stands proximate to the lake. On the

Olympic Peninsula, the ‘pollenshed’ includes a variety of topographic positions, slopes, and aspects that are known to favor different species, and a surface pollen study has shown significant contributions of low-elevation taxa to high elevations (Gavin et al. 2005). In contrast, LPJ-GUESS simulations occur on homogeneous, stand-sized patches.

Across all sites, the period of least agreement between simulation and pollen record is the early Holocene (11-9ka), the time of a solar insolation maximum. Pollen records from the Peninsula and from the broader region show an increased abundance of shade-intolerant species (Gavin et al. 2013). This has been explained by increased frequency of fire due to warmer and drier summers (Gavin, Brubaker, and Greenwald 2013). Charcoal records from lake sediments also indicate more frequent fire during this period. There are two plausible reasons why the simulations do not reflect the pollen records in the early Holocene. First, the input climate data may not capture the magnitude of warmth in early Holocene summers, though Trace-21 summer temperature anomalies from the present day are comparable to estimations from other climate proxies (Chase et al. 2008). Second, axial tilt and day and season length remain constant in LPJ-GUESS, so while the input climate data reflects orbital variations, calculation of direct solar radiation on a simulated patch does not. Together these inputs may explain why simulated soil moisture remains unrealistically high, fires infrequent, and shade-tolerant species dominant throughout the simulated early Holocene.

CHAPTER V

CONCLUSION

This study affirms the importance of exploring the effects of climate change on forests with methods that consider species interactions, transient dynamics, and functional components of the climate. For example, in order to understand how forests may respond to reduced snowpack, we must not only quantify the relationships between tree distributions and climate variables, but we must fully understand the transient processes by which distributions change (establishment and mortality) and the sensitivities of trees to specific components of the climate. Here we identify important climatic limits on tree establishment related to growing season length and intensity and moisture availability.

Attempts to reconstruct pollen records with process-based vegetation models provide valuable insight into the drivers of species-level change in forest communities at local to regional scales. Species parameters calibrated to simulate realistic present distributions with respect to elevation and precipitation gradients are also suitable for use in paleoecological simulations. Discrepancies between observed and simulated vegetation serve to highlight areas of limited understanding and focus future research efforts.

CHAPTER VI

REFERENCES CITED

Agee, J. K. 1996. *Fire Ecology of Pacific Northwest Forests*. Island Press.

Barbour, M. G., N. H. Berg, T. G. F. Kittel, and M. E. Kunz. 1991. “Snowpack and the Distribution of a Major Vegetation Ecotone in the Sierra Nevada of California.” *Journal of Biogeography*: 141–149.

Brown, K. J., and R. J. Hebda. 2002. “Origin, Development, and Dynamics of Coastal Temperate Conifer Rainforests of Southern Vancouver Island, Canada.” *Canadian Journal of Forest Research* 32 (2): 353–372.

Chan, S. S., S. R. Radosevich, and A. T. Grotta. 2003. “Effects of Contrasting Light and Soil Moisture Availability on the Growth and Biomass Allocation of Douglas-fir and Red Alder.” *Canadian Journal of Forest Research* 33 (1): 106–117.

COHMAP Members. 1988. “Climatic Changes of the Last 18,000 Years: Observations and Model Simulations.” *Science* 241 (4869) (August 26): 1043–1052. doi:10.2307/1702404.

Compo, G. P., J. S. Whitaker, P. D. Sardeshmukh, N. Matsui, R. J. Allan, X. Yin, B. E. Gleason, et al. 2011. “The Twentieth Century Reanalysis Project.” *Quarterly Journal of the Royal Meteorological Society* 137 (654): 1–28. doi:10.1002/qj.776.

Cwynar, L.C. 1987. “Fire and Forest History of the North Cascade Range.” *Ecology* 68: 791–802.

Daly, C., M. Halbleib, J. I. Smith, W. P. Gibson, M. K. Doggett, G. H. Taylor, J. Curtis, and P. P. Pasteris. 2008. “Physiographically Sensitive Mapping of Climatological Temperature and Precipitation Across the Conterminous United States.” *International Journal of Climatology* 28 (15) (December): 2031–2064. doi:10.1002/joc.1688.

Davis, M. B. 1963. “On the Theory of Pollen Analysis.” *American Journal of Science* 261 (10): 897–912.

Duursma, R. A., J. D. Marshall, J. B. Nippert, C. C. Chambers, and A. P. Robinson. 2005. “Estimating Leaf-level Parameters for Ecosystem Process Models: a Study in Mixed Conifer Canopies on Complex Terrain.” *Tree Physiology* 25 (11): 1347–1359.

Ettinger, A. K., K. R. Ford, and J. HilleRisLambers. 2011. “Climate Determines Upper, but Not Lower, Altitudinal Range Limits of Pacific Northwest Conifers.” *Ecology* 92 (6): 1323–1331.

Fischer, W. C., and A. F. Bradley. 1987. “Fire Ecology of Western Montana Forest Habitat Types”. United Stated Forest Service General Technical Report INT-223.

Fonda, R.W., and L.C. Bliss. 1969. “Forest Vegetation of the Montane and Subalpine Zones, Olympic Mountains, Washington.” *Ecological Monographs* 39: 271–301.

Franklin, J. E., and C. T. Dyrness. 1988. *Natural Vegetation of Oregon and Washington*. Oregon State University Press.

Gavin, D. G., L. B. Brubaker, and D. N. Greenwald. 2013. “Postglacial Climate and Fire-Mediated Vegetation Change on the Western Olympic Peninsula, Washington.” *Ecological Monographs* (April 18). doi:10.1890/12-1742.1.

Gavin, D. G., D. M. Fisher, E. M. Herring, A. White, and L. B. Brubaker. 2013. “Paleoenvironmental Change on the Olympic Peninsula, Washington: Forests and Climate from the Last Glaciation to the Present.” Report on file at the Olympic National Park, Port Angeles, WA.

Gavin, D.G., L.B. Brubaker, J.S. McLachlan, and W.W. Oswald. 2005. “Correspondence of Pollen Assemblages with Forest Zones Across Steep Environmental Gradients, Olympic Peninsula, Washington, USA.” *The Holocene* 15 (5) (July): 648–662.

Gavin, D.G., J.S. McLachlan, L.B. Brubaker, and K.A. Young. 2001. “Postglacial History of Subalpine Forests, Olympic Peninsula, Washington, USA.” *Holocene* 11 (2): 177–188.

Gerten, D., S. Schaphoff, U. Haberlandt, W. Lucht, and S. Sitch. 2004. “Terrestrial Vegetation and Water Balance—hydrological Evaluation of a Dynamic Global Vegetation Model.” *Journal of Hydrology* 286 (1): 249–270.

Haxeltine, A., and I. C. Prentice. 1996. “BIOME3: An Equilibrium Terrestrial Biosphere Model Based on Ecophysiological Constraints, Resource Availability, and Competition Among Plant Functional Types.” *Global Biogeochemical Cycles* 10 (4): 693–709.

He, F. 2010. “Simulating Transient Climate Evolution of the Last Deglaciation with CCSM3”. University of Wisconsin. http://www.cgd.ucar.edu/ccr/paleo/Notes/TRACE/he_phd_092010-1.pdf.

Henderson, J.A., R.D. Lesher, D.H. Peter, and C.D. Ringo. 2011. “A Landscape Model for Predicting Potential Natural Vegetation of the Olympic Peninsula USA Using Boundary Equations and Newly Developed Environmental Variables”. USDA General Technical Report: PNW-GTR-941. USDA Forest Service.

Henderson, J.A., D.H. Peter, R.D. Lesher, and D.C. Shaw. 1989. “Forested Plant Associations of the Olympic National Forest”. R6 ECOL Technical Paper 001-88. USDA Forest Service.

Hickler, T., B. Smith, M. T Sykes, M. B Davis, S. Sugita, and K. Walker. 2004. “Using a Generalized Vegetation Model to Simulate Vegetation Dynamics in Northeastern USA.” *Ecology* 85 (2): 519–530.

Hickler, T., K. Vohland, J. Feehan, P. A. Miller, B. Smith, L. Costa, T. Giesecke, et al. 2012. “Projecting the Future Distribution of European Potential Natural Vegetation Zones with a Generalized, Tree Species-based Dynamic Vegetation Model.” *Global Ecology and Biogeography* 21 (1) (January): 50–63. doi:10.1111/j.1466-8238.2010.00613.x.

Kellndorfer, J. M., W. S. Walker, E. LaPoint, K. Kirsch, J. Bishop, and G. Fiske. 2010. “Statistical Fusion of Lidar, InSAR, and Optical Remote Sensing Data for Forest Stand Height Characterization: A Regional-scale Method Based on LVIS, SRTM, Landsat ETM+, and Ancillary Data Sets.” *Journal of Geophysical Research: Biogeosciences (2005–2012)* 115 (G2).

Kershaw Jr, J. A., and D. A. Maguire. 1995. “Crown Structure in Western Hemlock, Douglas-fir, and Grand Fir in Western Washington: Trends in Branch-level Mass and Leaf Area.” *Canadian Journal of Forest Research* 25 (12): 1897–1912.

Krumhardt, K. M., and J. O. Kaplan. 2010. “ARVE Technical Report# 2: A Spline Fit to Atmospheric CO2 Records from Antarctic Ice Cores and Measured Concentrations for the Past 25,000 Years.” *Environmental Engineering Institute, Ecole Polytechnique Fédérale de Lausanne, Lausanne, Switzerland*.

Leemans, R., and I. C. Prentice. 1989. “FORSKA-a General Forest Succession Model.” *Meddelanden Fraan Växtbiologiska Institutionen*.

Littell, J.S., E.E. Oneil, D. McKenzie, J.A. Hicke, J.A. Lutz, R.A. Norheim, and M.M. Elsner. 2010. “Forest Ecosystems, Disturbance, and Climatic Change in Washington State, USA.” *Climatic Change* 102 (1): 129–158.

Littell, J.S., D.L. Peterson, and M. Tjoelker. 2008. “Douglas-fir Growth in Mountain Ecosystems: Water Limits Tree Growth from Stand to Region.” *Ecological Monographs* 78 (3) (August): 349–368.

Liu, Z., B. L. Otto-Bliesner, F. He, E. C. Brady, R. Tomas, P. U. Clark, A. E. Carlson, et al. 2009. “Transient Simulation of Last Deglaciation with a New Mechanism for Bolling-Allerod Warming.” *Science* 325 (5938) (July 16): 310–314. doi:10.1126/science.1171041.

Martínez-Vilalta, J., A. Sala, and J. Piñol. 2004. “The Hydraulic Architecture of Pinaceae–a Review.” *Plant Ecology* 171 (1-2): 3–13.

McKenzie, D., D. W. Peterson, D. L. Peterson, and P. E. Thornton. 2003. “Climatic and Biophysical Controls on Conifer Species Distributions in Mountain Forests of Washington State, USA.” *Journal of Biogeography* 30 (7) (July): 1093–1108.

McLachlan, J., and L.B. Brubaker. 1995. “Local and Regional Vegetation Change on the Northeastern Olympic Peninsula During the Holocene.” *Canadian Journal of Botany* 73: 1618–1627.

Miller, P. A, T. Giesecke, T. Hickler, R. H.W Bradshaw, B. Smith, H. Seppä, P. J Valdes, and M. T Sykes. 2008. “Exploring Climatic and Biotic Controls on Holocene Vegetation Change in Fennoscandia.” *Journal of Ecology* 96 (2): 247–259.

Mitchell, A. K. 2001. “Growth Limitations for Conifer Regeneration Under Alternative Silvicultural Systems in a Coastal Montane Forest in British Columbia, Canada.” *Forest Ecology and Management* 145 (1): 129–136.

Nakawatase, J. M., and D. L. Peterson. 2006. “Spatial Variability in Forest Growth - Climate Relationships in the Olympic Mountains, Washington.” *Canadian Journal of Forest Research* 36 (1) (January): 77–91. doi:10.1139/X05-224.

Ni, Jian, Sandy P. Harrison, I. Colin Prentice, John E. Kutzbach, and Stephen Sitch. 2006. “Impact of Climate Variability on Present and Holocene Vegetation: a Model-based Study.” *Ecological Modelling* 191 (3): 469–486.

Niinemets, Ü., and F. Valladares. 2006. “Tolerance to Shade, Drought, and Waterlogging of Temperate Northern Hemisphere Trees and Shrubs.” *Ecological Monographs* 76 (4): 521–547.

Nolin, A. W., and C. Daly. 2006. “Mapping ‘at Risk’ Snow in the Pacific Northwest.” *Journal of Hydrometeorology* 7 (5) (October): 1164–1171. doi:10.1175/JHM543.1.

Peterson, D.L., E.G. Schreiner, and N.M. Buckingham. 1997. “Gradients, Vegetation and Climate: Spatial and Temporal Dynamics in the Olympic Mountains, USA.” *Global Ecology and Biogeography Letters* 6: 7–17.

Prentice, I. C., W. Cramer, S. P. Harrison, R. Leemans, R. A. Monserud, and A. M. Solomon. 1992. “Special Paper: a Global Biome Model Based on Plant Physiology and Dominance, Soil Properties and Climate.” *Journal of Biogeography*: 117–134.

Prentice, I. C., S. P. Harrison, and P. J. Bartlein. 2011. “Global Vegetation and Terrestrial Carbon Cycle Changes after the Last Ice Age.” *New Phytologist* 189 (4): 988–998.

Prentice, I.C., P.J. Bartlein, and T. Webb III. 1991. “Vegetation and Climate Change in Eastern North America Since the Last Glacial Maximum.” *Ecology*: 2038–2056.

Prentice, I.C., M. T. Sykes, and W. Cramer. 1993. “A Simulation Model for the Transient Effects of Climate Change on Forest Landscapes.” *Ecological Modelling* 65 (1): 51–70.

Rasmussen, L. A., H. Conway, and P. S. Hayes. 2000. “The Accumulation Regime of Blue Glacier, USA, 191496.” *Journal of Glaciology* 46 (153): 326–334.

Salathé, E. P., L. R. Leung, Y. Qian, and Y. Zhang. 2010. “Regional Climate Model Projections for the State of Washington.” *Climatic Change* 102 (1-2) (May 5): 51–75. doi:10.1007/s10584-010-9849-y.

Shuman, B., P. Newby, Y. Huang, and T. Webb III. 2004. “Evidence for the Close Climatic Control of New England Vegetation History.” *Ecology* 85 (5): 1297–1310.

Sitch, S., B. Smith, I.C. Prentice, A. Arneth, A. Bondeau, W. Cramer, J.O. Kaplan, et al. 2003. “Evaluation of Ecosystem Dynamics, Plant Geography and Terrestrial Carbon Cycling in the LPJ Dynamic Global Vegetation Model.” *Global Change Biology* 9 (2): 161–185.

Smith, B., I.C. Prentice, and M.T. Sykes. 2001. “Representation of Vegetation Dynamics in the Modelling of Terrestrial Ecosystems: Comparing Two Contrasting Approaches Within European Climate Space.” *Global Ecology and Biogeography* 10 (6): 621–637.

Soll, J.A. 1994. “Seed Number, Germination and First Year Survival of Subalpine Fir (Abies Lasiocarpa) in Subalpine Meadows of the Northeastern Olympic Mountains”. M.S. Thesis, Seattle: University of Washington.

Stephenson, N. 1998. “Actual Evapotranspiration and Deficit: Biologically Meaningful Correlates of Vegetation Distribution Across Spatial Scales.” *Journal of Biogeography* 25 (5): 855–870.

Tang, G., B. Beckage, and B. Smith. 2012. “The Potential Transient Dynamics of Forests in New England Under Historical and Projected Future Climate Change.” *Climatic Change* 114 (2) (February 8): 357–377. doi:10.1007/s10584-012-0404-x.

Thackray, G.D. 2001. “Extensive Early and Middle Wisconsin Glaciation on the Western Olympic Peninsula, Washington, and the Variability of Pacific Moisture Delivery to the Northwestern United States.” *Quaternary Research* 55 (3): 257–270.

Thompson, R. S., K. H. Anderson, and P. J. Bartlein. 1999. “Atlas of Relations Between Climatic Parameters and Distributions of Important Trees and Shrubs in North America”. Professional paper 1650 A & B. Denver (CO): US Geological Survey. http://pubs.usgs.gov/pp/p1650-b/.

Townend, J. 1995. “Effects of Elevated CO2, Water and Nutrients on Picea Sitchensis (Bong.) Carr Seedlings.” *New Phytologist* 130 (2): 193–206.

Turner, D. P., S. A. Acker, J. E. Means, and S. L. Garman. 2000. “Assessing Alternative Allometric Algorithms for Estimating Leaf Area of Douglas-fir Trees and Stands.” *Forest Ecology and Management* 126 (1): 61–76.

Urban, D. L., M. E. Harmon, and C. B. Halpern. 1993. “Potential Response of Pacific Northwestern Forests to Climatic Change, Effects of Stand Age and Initial Composition.” *Climatic Change* 23 (3): 247–266.

Walker, I. R., and M. G. Pellatt. 2008. “Climate Change and Ecosystem Response in the Northern Columbia River Basin — A Paleoenvironmental Perspective.” *Environmental Reviews* 16 (NA) (December): 113–140. doi:10.1139/A08-004.

Wang, T., A. Hamann, D. L. Spittlehouse, and T. Q. Murdock. 2012. “ClimateWNA-High-resolution Spatial Climate Data for Western North America.” *Journal of Applied Meteorology and Climatology* 51 (1): 16–29.

Waring, R. H., P. E. Schroeder, and R. Oren. 1982. “Application of the Pipe Model Theory to Predict Canopy Leaf Area.” *Canadian Journal of Forest Research* 12 (3): 556–560.

Webb, T. 1986. “Is Vegetation in Equilibrium with Climate? How to Interpret late-Quaternary Pollen Data.” *Plant Ecology* 67 (2) (October): 75–91. doi:10.1007/BF00037359.

White, M. A., P. E. Thornton, S. W. Running, and R. R. Nemani. 2000. “Parameterization and Sensitivity Analysis of the BIOME-BGC Terrestrial Ecosystem Model: Net Primary Production Controls.” *Earth Interactions* 4 (3): 1–85.

Whitlock, C. 1992. “Vegetational and Climatic History of the Pacific Northwest During the Last 20,000 Years: Implications for Understanding Present Day Biodiversity.” *Northwest Environmental Journal* 8: 5–28.

Woodward, A., E.G. Schreiner, and D.G. Silsbee. 1995. “Climate, Geography and Tree Establishment in Subalpine Meadows of the Olympic Mountains, Washington, USA.” *Arctic and Alpine Research* 27: 217–225.

Woodward, F.I. 1987. *Climate and Plant Distribution*. Cambridge Studies in Ecology. Cambridge University Press.

Zolbrod, A.N., and D.L. Peterson. 1999. “Response of High-elevation Forests in the Olympic Mountains to Climatic Change.” *Canadian Journal of Forest Research* 29 (12): 1966–1978.