Historical aerial photos were used to examine the early phase of forest succession after stand replacement disturbance, covering the Coast Ranges Province (CRP) and the western Cascades Province (WCP) of western Oregon. The study consisted of two components: characterizing the pattern of forest succession in western Oregon; analyzing the influence of climatic and physiographic factors on forest succession.

Succession has many dimensions. In this study, I examined succession after stand replacement disturbance in terms of canopy cover change of different life forms: shrubs, hardwood trees, and conifer trees. Canopy cover changes from 1959 to 1997 for selected sample stands were obtained by photo interpretation. Canopy cover growth curves for each sample stand were developed based on a Chapman-Richards growth function. Seven successional pathways were defined to characterize forest successional processes based on projected canopy cover at age 50 and the process of canopy composition change over this 50 years period. In addition, seven parameters from the canopy cover growth curves were...
derived for the purpose of comparison of successional patterns in the CRP and WCP. These include time to reach 5% and 70% of canopy cover, weighted mean absolute growth rate, weighted mean relative growth rate, maximum absolute growth rate, time to reach maximum absolute growth rate, and active growth period. Results indicated that a wide range of variation in forest succession exists in western Oregon. Successional patterns for the CRP and WCP were different in terms of conifer development.

Possible abiotic controls of two successional parameters were examined by stepwise regression analysis. Only 23%, 37%, and 29% of the total variation in the delay, and 29%, 25% and 57% of the total variation in rate parameters can be explained by abiotic factors for the WCP, CRP, and across provinces, respectively. Unexplained variation was likely due to stochastic, biotic, and management factors, as well as experimental error due to photo interpretation and derivation of successional parameters. The most important influential climatic factor was temperature, and the most important physiographic factor was elevation. Depending on location, interactions among climatic and physiographic factors also influenced successional delay and rate.
Early Forest Succession Following Clearcuts in Western Oregon: Patterns and Abiotic Controls

by
Zhiqiang Yang

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Zhiqiang Yang, Author
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LIST OF ACRONYMS

AGP  active growth period
CB   closed broadleaf stage
CC   closed conifer stage
CM   closed mixed stage
CONTPRE mean percentage of annual precipitation in June-August
CRP  Coast Ranges Province
DELAY time to reach 5% cover
DEM  digital elevation model
EASTNESS sin(aspect)
ELEV elevation
FROSTDAY mean number of days with minimum temperature below 0°C in one year
MaxRate maximum absolute growth rate
NORAIN mean number of days without precipitation in one year
OP   open stage
PNW  Pacific Northwest
PRCP mean daily precipitation
RSP  relative slope position
SH   shrub stage
SC   semi-closed stage
SLOPE slope
SMRPRCP mean daily precipitation in May – September
SMRTMP mean daily temperature in May – September
SMRTSMRP moisture stress during the growing season
SOUTHNESS cos(aspect + 180)
SRAD mean daily potential solar radiation
RATE weighted mean absolute growth rate
LIST OF ACRONYMS (Continued)

T70                time to reach 70% cover
TDAY               mean daily precipitation
TMAX               maximum daily maximum temperature
TmaxRate           time to reach maximum absolute growth rate
TMIN               minimum daily minimum temperature
TRANSASP           cos(45-aspect)+1
TRMI               topographic relative moisture index
VPD                mean daily water vapor pressure
WCP                Western Cascades Province
wmAGR              weighted mean absolute growth rate
wmRGR              weighted mean relative growth rate
WTRPRCP            mean daily precipitation in November – March
WTRTMP             mean daily temperature in November – March
Early Forest Succession Following Clearcuts in Western Oregon: Patterns and Controls

Chapter 1 Introduction

Understanding forest succession is critical for forest ecosystem management and biodiversity conservation planning (Knight and Wallace, 1989). In particular, successional pathway and rate have important implications for biogeochemical cycling of nitrogen (Pastor and Post, 1986) and carbon (Botkin and Running, 1984; Harmon, 2001a, b).

After stand replacement disturbance in the Pacific Northwest (PNW) region of the United States, forest succession generally leads to a closed canopy conifer condition (Franklin and Dyrness, 1988). However, the rate and density of conifer recovery can vary significantly across the region (Franklin and Hemstrom, 1981; Nesje, 1996; Tappeiner et al., 1997; Poage, 2001). Many studies in PNW have investigated the problem of conifer regeneration failure and it has been widely recognized that numerous factors contribute to successional variation. However, most of these studies were based on a field survey of sample plots over a small spatial extend, and results among these studies are inconsistent.

The purpose of this study was to add to our understanding of early forest succession in western Oregon by examining forest canopy
development. To that purpose, I try to answer the following questions about forest succession after stand replacement disturbance in western Oregon:

(1) How variable is secondary succession in western Oregon?

(2) What are the controlling abiotic factors on the variation in forest succession?

Succession is a term used to describe many aspects of vegetation change over different scales of space and time. In this study, succession was studied in western Oregon by focusing on two components: 1) the temporal directional change of forest stand composition and vegetation physiognomy, and 2) the rate of conifer cover accumulation.

My examination of forest succession in western Oregon consists of two major components, reported in the two main chapters of this dissertation. While ground level works provide details for one location, the use of historical aerial photographs and a geographic information system makes the study of forest succession patterns over western Oregon feasible. Through examination of forest canopy change over time, I was able to characterize forest successional patterns in western Oregon. Moreover, by exploring various abiotic factors that might control forest succession, we can achieve a better understanding of forest successional processes in western Oregon.

In chapter 2, I examined patterns of succession in western Oregon using historical aerial photos. To characterize succession, I defined a set of
successional pathways based on projected canopy cover and the canopy composition change over time, which enable me to compare forest succession among sample stands distributed over landscape. From photo interpretation, vegetation change for each site was recorded as proportions of vegetation life forms. Classes of successional trajectory were developed which encompass rates, temporal patterns, and directions of change. From these data, I was able to establish the frequency distribution of slow, normal and fast rates toward canopy closure.

Chapter 3 reports the results of my analysis of abiotic factors controlling forest succession processes in western Oregon, focusing on two successional parameters defined in Chapter 2: DELAY and RATE. The explanatory variables examined were mainly climatic and phygiographic factors. These variables were examined using stepwise regression to determine which variables were important in explaining the patterns observed in Chapter 2.
Chapter 2  Patterns of Early Forest Succession Following Clearcuts in Western Oregon

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January 12, 2004
2.1 ABSTRACT

In the Pacific Northwest (PNW), the pattern of conifer development after stand-replacement disturbance has important implications for many forest processes (e.g. carbon storage, nutrient cycling, biodiversity). This chapter examines conifer development in the Coast Ranges Province (CRP) and the Western Cascades Province (WCP) of Oregon using historic aerial photographs. Ninety-four stands from the WCP and 59 stands from CRP were photo-interpreted from 1959 to 1997 in roughly 5 year intervals. A Chapman-Richards growth function was used to model conifer cover development for all sample stands. Based on the photo data and Chapman-Richards function, these stands were classified into one of seven early forest successional pathways. The interaction of successional pathway and rate, i.e. rate of conifer cover accumulation, was used to classify stands into 9 different successional trajectories. Successional trajectories in the CRP and WCP were compared using the set of seven parameters derived from the Chapman-Richards growth function. Our results echo previous studies in that rates and densities of conifer regeneration varied markedly among sites. Results also indicate that early forest succession patterns are different for the two study regions in terms of both pathway and trajectories. Conifer regeneration in the WCP tends to have longer delay and lower rate of development compared to the CRP. We conclude by briefly examining
climatic, biotic, and management factors that might influence successional trajectories in western Oregon.
2.2 INTRODUCTION

There is a growing demand for landscape-scale information on forest successional trends and factors that contribute to divergence of successional trajectories. Increasingly, spatial models are being used for regional planning and research efforts. Model output, for example, might include current and future estimates of biodiversity or biogeochemical fluxes. Models requiring future status for individual forest stands use data on the projected rate and pathway of succession for parameterization and/or validation (Hall, 1991). For example, the overall carbon budget for a coniferous stand is dependent on the time since disturbance for decomposition of detritus and for the amount of live biomass accumulated. In such a system, if rates of conifer establishment are variable, carbon dynamics will also be variable (Harmon et al., 1990). As very little work has been done to characterize successional variability across a landscape or region, models commonly assume an average rate of forest succession and growth (Cohen et al., 1996).

Succession is a term used to describe many aspects for vegetation change over different scales of space and time. Here we study early conifer forest succession in western Oregon focusing on two components: 1) the temporal directional change of forest stand composition and vegetation physiognomy, and 2) the rate of conifer cover accumulation. The causes of
these changes are related to natural as well as human influenced processes.

In the Pacific Northwest (PNW) region of the United States, the order of potential vegetation transitions at a site is generally predictable, with larger growth forms replacing smaller ones (e.g. shrubs replacing grass and trees replacing shrubs). However, the rates and specific pathways of succession can vary considerably among sites. For example, after wildfire in this coniferous region, some stands may go directly from recolonizing shrubs to hardwood trees for an extended period before eventually returning to conifer condition. Other stands might go rapidly and directly from shrub condition to conifer condition (Franklin and Dyrness, 1988, Halpern, 1988). In commercially harvested stands, there are often more extremes of pattern with examples of highly accelerated and severely stagnated stands not uncommon (Perry et al., 1989).

In this paper, we use historical aerial photos to examine secondary forest succession after stand replacement disturbance in terms of canopy cover change of different life forms: shrubs, hardwood trees, and conifer trees. The main objectives were to: (1) verify the existence of divergent trajectories of early succession among harvested stands in western Oregon, (2) develop a method for quantifying successional pathway and rate, and (3) compare early forest successional trajectories between the
Coast Ranges Province (CRP) and Western Cascades Province (WCP) (Figure 2.1).

2.3 STUDY AREA

The study area is the portions of the CRP and WCP of western Oregon contained in Landsat TM path/row 46/29 (Figure 2.1). Since the availability of historical aerial photos varies, but is most extensive over National Forest lands, stands from the Siuslaw National Forest in CRP and Willamette National Forest in WCP were used.

Figure 2.1 Digital elevation model of study area. Portion of the Siuslaw National Forest and Willamette National Forest contained within Landsat TM, Aug. 19, 1995  Path 46, Row 29
2.3.1 Physical Environment

The Pacific Northwest region has a climate of warm, dry summers and mild, wet winters. These climate conditions favor growth of evergreen life forms. The climate exhibits a strong gradient with change of latitude, longitude, and elevation.

The CRP is characterized by mild temperature with prolonged cloudy periods. The average temperature ranges from 5 °C in January to 16 °C in July. Annual precipitation in the CRP is about 3000 mm. Depending on location, summers in the CRP range from cool to warm. Elevations generally vary in the range of 450-750 meters in the CRP. The climate of WCP is also maritime with mild, wet winters and warm, dry summers. Average temperature ranges from -5 °C in January to 23 °C in July. Annual precipitation in the CRP is about 2300mm. Elevations in the WCP vary in the range of 450-3100 meters.

Geologic conditions are different for CRP and WCP. Sedimentary rock types are typical of the CRP, while the volcanic rocks dominate most of the WCP. Forest soils vary in the two regions, reflecting the variation in parent materials and topography (Franklin and Dyrness, 1988).

2.3.2 Vegetation

In contrast to other moist and mesic regions in the world where hardwood typically dominates, PNW forests have a ratio of coniferous to hardwood of 1000:1 (Kuchler, 1964). Moreover, forests in PNW are
characterized as having among the greatest biomass accumulations and some of the highest productivity level forests on earth (Waring and Franklin, 1979). Two major forest vegetation zones exist in the study area (Franklin and Dyrness, 1988). The CRP consists of the Sitka Spruce Zone and the Western Hemlock Zone, and WCP consists of the Western Hemlock Zone. Dominant trees are typically conifers, except in riparian areas where hardwood trees often dominate. Besides conifer and hardwood trees, many different shrub and herbaceous species exist in the study area.

2.4 METHODS

2.4.1 Data Acquisition

Previous studies indicate that elevation and aspect interact to affect conifer development in the H.J. Andrews Experimental Forest (Nesje 1996), the most studied location in the region. Therefore to collect data for this study, we classified the study area into 8 aspect classes (45 degree intervals) and 6 elevation classes (300 meter intervals) using 30 meter DEM data, for a total of 48 aspect-elevation classes. Topographic facets with less than 36 DEM cells (2.25 hectares) were removed from the potential sample area. This ensured that the final samples had at least a 25m buffer around them. Stratified random sampling from the 48 classes with an average of 5 samples per class yielded a potential sample size of 240 1-ha stands. Of these, 94 were selected from WCP and 59 were selected from CRP based
on the availability of aerial photographs. Most of the aerial photos used were color having various scales (Table 2.1).

Table 2.1 Historical aerial photos used for photo interpretation.

<table>
<thead>
<tr>
<th>WCP</th>
<th>CRP</th>
</tr>
</thead>
<tbody>
<tr>
<td>1959*</td>
<td>1961/1962*</td>
</tr>
<tr>
<td>1967**</td>
<td>1968/1969**</td>
</tr>
<tr>
<td>1972***</td>
<td>1972**</td>
</tr>
<tr>
<td>1979*</td>
<td>1979*</td>
</tr>
<tr>
<td>1988***</td>
<td>1984*</td>
</tr>
<tr>
<td>1990*</td>
<td>1989*</td>
</tr>
<tr>
<td>1997*</td>
<td>1993/1995*</td>
</tr>
</tbody>
</table>

b: black and white photo; otherwise color photo
* 1:12000; ** 1:15840; *** 1:40000

By photo interpretation, percent cover of conifer trees, hardwood trees, shrub/grass, and open condition was determined for each 1-ha sample stand (Avery and Berlin, 1985). For WCP samples, stand origin dates were obtained from the VEGIS database (Willamette National Forest 2001). For CRP samples, origin dates were obtained from the VEGE arc-coverage (Siuslaw National Forest, 1992).

2.4.2 Fitting Vegetation Cover Growth Curves

The stand origin and duration of photo-interpreted period varied among sample stands in the study area, thus, it was hard to make direct comparison among stands without normalization. To normalize the photo-interpreted data, cover proportions were modeled as a function of time since stand origin using a mathematical growth function. Historically, various growth functions have been used, including monomolecular
(Gregory, 1928), logistic (Reed & Holland, 1919, Robertson, 1923), and Chapman-Richards (Richards, 1969; Causton et al., 1978). See Richards (1969) for an extensive review of various growth functions. We choose the Chapman-Richards function as it could accommodate the wide range of shapes existing in our data. A Chapman-Richards function (Richards 1959, Hunt 1982, Ratkowsky 1990) has the form of

\[ f(t) = A \times (1 - e^{-kt})^b \]  

where \( f(t) \) is the canopy cover at time \( t \), \( A \) is the asymptotic maximum value (the theoretical maximum size), \( b \) describes the shape of the fitted curve, \( c \) positions the curve in relation to the time axis, and \( k \) is a rate-constant whose interpretation depends on the value of \( b \). Based on the assumption that all stands will eventually reach 100 percent canopy cover asymptotically and the initial percentage cover was 0 percent, \( A \) and \( c \) were assumed to be 100 and 0 respectively. Therefore, a simplified function was used to model canopy cover change for each sample stand:

\[ f(t) = 100 \times (1 - e^{-kt})^b \]  

Stands defining the trajectory envelope for each province were identified to highlight the variability of conifer accumulation in each province. To characterize cross-sample variability, percentage cover as a function of time since stand origin (up to 50 years) was modeled separately for each sample stand using SAS (SAS, 1999). The parameters of each
“trajectory” regression were defined for both percent conifer cover and for percentage tree cover (conifer and hardwood combined).

2.4.3 Successional Pathways

Successional pathway after stand replacement disturbance is defined here as the shift over time in vegetation from ephemeral herbaceous life-forms, to taller perennial herbs and shrubs to either hardwood trees, conifer trees, or a mixture of the two (Franklin and Dyrness 1988, Perry et al. 1989). The process of vegetation shifts are influenced by both natural forest regeneration and human activities like planting and stand management. For this study we classified successional pathways into these stages as described in Table 2.2. The open stage (OP) occurs immediately after stand replacement disturbance, at which time grasses and herbaceous plants quickly occupy a site. The OP stage transitions to the shrub stage (SH) until tree cover reaches between 30 and 70%, at which time it is defined as in a semi-closed stage (SC). During the SC stage, the dominant life form can switch between conifer, broadleaf, and a mixture of the two. At the time of canopy closure (70% or greater tree cover), a stand will be dominated by conifer trees (CC), broadleaf trees (CB), or in a mixed condition (CM). If a closed conifer stand was mixed or dominated by broadleaf trees when in the SC stage, it is designated as CC II, otherwise it is designated CC I. Likewise, if a CB stands was mixed or dominated by conifer during the SC stage, it is designated as pathway CB II, otherwise it
is designated CB I. Stands reaching the CM stage may have been in mixed or pure tree condition during the SC stage, but were in a mixed condition at age 50.

Table 2.2 Definitions of successional pathway stages.

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Name</th>
<th>% Tree Cover</th>
<th>% Conifer or % Hardwood</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>OP</td>
<td>Open</td>
<td>0</td>
<td>N/A</td>
<td>Usually the initial stage after stand replacement disturbance.</td>
</tr>
<tr>
<td>SH</td>
<td>Shrub &amp; Herb</td>
<td>&lt;30</td>
<td>Variable</td>
<td>Tree cover is less than 30%.</td>
</tr>
<tr>
<td>SC</td>
<td>Semi-closed</td>
<td>30-70</td>
<td>Variable</td>
<td>Tree cover is between 30-70%.</td>
</tr>
<tr>
<td>CC (I, II)</td>
<td>Closed Conifer</td>
<td>&gt;70</td>
<td>Conifer &gt;70%</td>
<td>Total tree cover is greater than 70% with more than 70% of tree cover being conifer. I or II indicates a stand in different condition during the SC stage (see text).</td>
</tr>
<tr>
<td>CB (I, II)</td>
<td>Closed Broadleaf</td>
<td>&gt;70</td>
<td>Broadleaf &gt; 70%</td>
<td>Total tree cover is greater than 70% with more than 70% of tree cover being broadleaf. I or II indicates a stand in different condition during the SC stage (see text).</td>
</tr>
<tr>
<td>CM</td>
<td>Closed Mixed</td>
<td>&gt;70</td>
<td>30%&lt;Conifer or Broadleaf &lt;70%</td>
<td>Total tree cover is greater than 70%. Both broadleaf and conifer tree are within the range of 30 to 70% of total tree cover.</td>
</tr>
</tbody>
</table>
Figure 2.2 shows the boundary conditions defining seven basic successional pathway categories ((OP is not considered as a pathway) in Table 2.2. Stands following successional pathway SH do not reach 30% tree cover within 50 years after disturbance (lower curve, Figure 2.2a). Similarly, stands in the SC category have total tree cover between 30 and 70% at age 50 (upper curve, Figure 2.2a). In both Figure 2.2b and 2.2c, the top lines represent total tree canopy cover. The lower line in Figure 2.2b represents 30% of the top line and the lower line in Figure 2.2c represents 70% of the top line. In both Figures 2.2b and 2.2c, the areas under the lower line represent the proportion of broadleaf cover. A stand belongs to CC I if the proportion of conifer cover is always above 30% of total tree cover. Otherwise, it belongs to CC II (Figure 2.2b). A stand belongs to CB I if the proportion of broadleaf tree cover is always greater than 30% of total tree cover. Otherwise, it belongs to CB II. In Figure 2.2d, the lower line and the middle line are 30% and 70% of total tree cover respectively. A stand belongs to CM if both proportions of conifer and broadleaf tree cover are within the 30% and 70% of the total tree cover.

To precisely describe the successional pathways for the sampled stands, the actual photo-interpretation data were used together with the modeled stage at 50 years since disturbance. That is, successional stage before age 50 for each stand was determined from photo interpretation as
this is the most accurate information available. As not all samples stands had reached 50 years since disturbance, the modeled successional stages at age 50 were used as the final reference stage for cross stand comparison.

![Figure 2.2 Boundary conditions for successional pathway categories](image)

**2.4.4 Successional Trajectories**

In this study, successional rate represents how fast conifer cover increased over time. Together with successional pathway, succession rate determines the successional trajectory. As such, successional trajectories for stands following the same pathway may be different due to differences
in rate. Since parameter $k$ and $b$ of the Chapman-Richard function do not have direct biological significance of their own and they have to be interpreted together, it is not useful to directly compare the differences between $k$ and $b$ values from Equation 2. Thus, to enable the characterization of variation in successional trajectories and comparison of trajectories between WCP and CRP, several parameters were derived from the Chapman-Richards function (Table 2.3) (Richard 1959, Causton and Venus 1981). DELAY is defined as the time to reach 5% canopy cover, which can be used to indicate whether growth stagnation has occurred after stand replacement disturbance. Weighted mean relative growth rate (wmRGR) and weighted mean absolute growth rate (wmAGR) were used to characterize the overall canopy development rate over the entire growth period. The maximum absolute growth rate (MaxRate) represents the potential maximum canopy development rate. More detailed discussion about the biological significance of these parameters was presented by Richards (1959). In addition to the above three direct measures of rate, we added three time-associated parameters which indirectly characterize succession rate. As canopy development rate eventually decreases with time, TmaxRate represents how quickly a stand will reaches its maximum absolute growth rate. T70 represents the time to reach closed canopy forest (70% cover), and AGP is the active growth period, the period in which conifer cover is continuously increasing.
Since conifer development was the main interest in this study, the parameters listed above were evaluated only for conifer cover of each sample stand. To compare the successional trajectories for CRP and WCP, the density distribution of the parameters from Table 2.3 were derived using S-plus (Insightful Corporation, 2001). The two regions were also compared in term of these parameters using a t-test.

Table 2.3 Successional trajectory parameters.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Formula</th>
<th>Detail</th>
</tr>
</thead>
<tbody>
<tr>
<td>DELAY</td>
<td>$\frac{\ln(1 - 0.05^{1/b})}{k}$</td>
<td>Time to reach 5% cover</td>
</tr>
<tr>
<td>wmRGR</td>
<td>$\frac{k}{b+1}$</td>
<td>Weighted mean relative growth rate</td>
</tr>
<tr>
<td>wmAGR</td>
<td>$\frac{A \times k}{2 \times (b+2)}$</td>
<td>Weighted mean absolute growth rate</td>
</tr>
<tr>
<td>MaxRate</td>
<td>$A \times k \times (1 - \frac{1}{b})^{k-1}$</td>
<td>Maximum absolute growth rate</td>
</tr>
<tr>
<td>TmaxRate</td>
<td>$\frac{\ln(b)}{k}$</td>
<td>Time to reach maximum absolute growth rate</td>
</tr>
<tr>
<td>T70</td>
<td>$\frac{\ln(1 - 0.7^{1/b})}{k}$</td>
<td>Time to reach 70% cover</td>
</tr>
<tr>
<td>AGP</td>
<td>T70 – DELAY</td>
<td>Active growth period</td>
</tr>
</tbody>
</table>

2.4.5 Classification of Successional Trajectories

Correlation analyses were conducted for the parameters listed in Table 2.3. To get the most independent parameters, the least correlated parameters were selected as classification criteria of successional trajectory. Based on the selected parameters, all sample stands were classified into three groups using the cross-province mean and standard
deviation of the parameter under consideration. If the value of the selected parameter is less than the mean minus one standard deviation of the parameter population, it belongs to group 1. If the selected parameter value is within one standard deviation of the mean, it belongs to group 2. If the selected parameter value is larger than the mean plus one standard deviation, it belongs to group 3. The classifications from each individual selected parameter were combined for the final classification.

2.5 RESULTS

2.5.1 General Successional Patterns

Scatter plots of conifer cover over time (Figure 2.3) indicate that there was a wide range of conifer cover accumulation over time among stands. Figure 2.4 shows the individual conifer accumulation models based on a Chapman-Richards growth function. This confirms that conifer accumulation over time is highly variable among stands, and showed that conifer cover accumulation for stands in CRP was generally faster than that in the WCP. In addition, Figure 2.4 also reveals that stands also varied in the time when conifer cover starts to accumulate more rapidly.

2.5.2 Successional Pathways

Photo interpretation revealed that in both the CRP and WCP, herbaceous vegetation quickly occupied a site immediately after stand replacement disturbance, although much of the herb cover was eventually replaced by trees. Examples of actual successional pathways based on
Figure 2.3 Scatter plots of conifer cover over time from the CRP (left) and WCP (right). The lines indicate the upper and lower envelope of the data cloud for the two sample areas by linking the extreme stand data.

Figure 2.4 Modeled conifer cover trajectories for the CRP (left) and WCP (right). Each line represents a single sample stand over time.

photo interpretation data were shown in Figure 2.5. Pathway models revealed that by age 50, the majority of sampled stands returned to CC stage in both provinces (CC I and CC II in Figure 2.6). However, in the WCP over 25% of stands had not returned to closed tree canopy condition, whereas in the CRP, all sampled stands returned to closed condition. In the CRP, nearly 7% of the sampled stands returned to a closed canopy broadleaf condition (CB I and CB II), and about 9% returned to a mixed
Figure 2.5 Examples of successional pathways. Data used were from photo interpretation of selected sample stands.
condition (CM). In the WCP, there were no sample stands that became closed broadleaf stands, but about 3% returned to a mixed forest condition.

These results indicate that disturbed forest stands return more quickly to closed tree condition in the CRP than in the WCP. However, hardwood trees were more likely to occur during early succession in the CRP than in the WCP. The results also indicate the existence of stands in WCP that may be returning to closed conditions very slowly (SH and SC in Figure 2.6).

Figure 2.6 Successional Pathway Distribution for CRP and WCP
2.5.3 Successional Trajectories

Based on the modeled growth curves (Figure 2.4), the distribution of successional trajectories varied both within province and across provinces. This was confirmed in Figure 2.7, which shows the distribution of successional trajectory parameters defined in Table 2.3, and Table 2.4 shows a summary of these distributions with time needed for the WCP was longer than the CRP.

Table 2.4 Comparison of Successional Trajectory Characteristics.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>WCP mean</th>
<th>std</th>
<th>CRP mean</th>
<th>std</th>
<th>p-value of t-test</th>
</tr>
</thead>
<tbody>
<tr>
<td>DELAY (years)</td>
<td>8.80</td>
<td>4.45</td>
<td>6.60</td>
<td>3.98</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>wmRGR (1/year)</td>
<td>0.12</td>
<td>0.06</td>
<td>0.22</td>
<td>0.08</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>wmAGR (%/year)</td>
<td>2.26</td>
<td>1.19</td>
<td>4.82</td>
<td>2.11</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>MaxRate (%/year)</td>
<td>3.36</td>
<td>1.74</td>
<td>7.12</td>
<td>3.09</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>TmaxRate (years)</td>
<td>18.20</td>
<td>7.72</td>
<td>12.4</td>
<td>8.88</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>T70 (years)</td>
<td>42.30</td>
<td>28.24</td>
<td>22.9</td>
<td>23.32</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>AGP (years)</td>
<td>33.50</td>
<td>27.67</td>
<td>16.2</td>
<td>20.94</td>
<td>&lt;0.01</td>
</tr>
</tbody>
</table>

Each of parameters in Table 2.3 had a significantly different distribution in each province (Figure 2.7) (Table 2.4). The variability of each parameter was of the same magnitude in both provinces (Table 2.4).

Sample stands in the WCP have longer DELAY than the CRP. Once a stand had reached 5% canopy cover, it generally showed a continuous increase in canopy cover (Figure 2.4). However, on average, stands were delayed about 7 years in the CRP, while they were delayed about 9 years in WCP (Table 2.4).
Figure 2.7 Distribution of successional trajectory parameters
Weighted mean relative growth rate (wmRGR), weighted mean absolute growth rate (wmAGR), and maximum absolute growth rate (MaxRate) were all highly correlated ($r$'s = 0.90-0.99) (Table 2.5). These three parameters have similar distribution both across provinces and within province (Figure 2.7). Student's t-tests indicated that all three parameters for conifer accumulation were significantly different (Table 2.4) between the WCP and CRP. For the CRP, wmAGR was more than twice that for stands in the WCP (2.26). Similar relationships exist between wmRGR and MaxRate for the WCP and CRP.

Table 2.5 Correlation Matrix for Successional Trajectory Characteristics*

<table>
<thead>
<tr>
<th></th>
<th>DELAY</th>
<th>wmRGR</th>
<th>wmAGR</th>
<th>MaxRate</th>
<th>TmaxRate</th>
<th>T70</th>
<th>AGP</th>
</tr>
</thead>
<tbody>
<tr>
<td>DELAY</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>wmRGR</td>
<td>-0.385</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>wmAGR</td>
<td>-0.169</td>
<td>0.904</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MaxRate</td>
<td>-0.178</td>
<td>0.912</td>
<td>0.999</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TmaxRate</td>
<td>0.880</td>
<td>-0.624</td>
<td>-0.441</td>
<td>-0.450</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>T70</td>
<td>0.391</td>
<td>-0.589</td>
<td>-0.640</td>
<td>0.592</td>
<td>-0.640</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>AGP</td>
<td>0.247</td>
<td>-0.556</td>
<td>-0.646</td>
<td>0.478</td>
<td>-0.645</td>
<td>0.988</td>
<td>1</td>
</tr>
</tbody>
</table>

*Units for the parameters are: DELAY (years), wmRGR (1/year), wmAGR (%/year), MaxRate (%/year), TmaxRate (years), T70 (years), AGP (years)

Time to reach maximum absolute growth rate (TmaxRate), time to reach 70% conifer cover (T70), and active growth period (AGP) showed similar pattern among sample stands both across and within provinces (Figure 2.7).

Of the succession parameters examined, the correlation of DELAY with succession rate (wmAGR) is the lowest ($r = -0.17$). T70 and AGP were
highly correlated and both were moderately correlated with TmaxRate. However, TmaxRate was closely related to DELAY. Based on these results, DELAY and wmAGR (hereafter referred to as RATE) were selected as successional trajectory descriptors and used to classify successional trajectories.

2.5.4 Successional Trajectory Classification

Using the group designation of the selected descriptors for all samples (i.e. across provinces), DELAY was clustered into three categories (short, medium, and long) (Table 2.6). Likewise, RATE was also clustered into three categories (slow, moderate, and fast).

Table 2.6 Successional trajectory classification criteria. Mean value of DELAY was 8.0 years with standard deviation of 4.4 years. Mean value of wmAGR was 3.2 with standard deviation of 2.0 years.

<table>
<thead>
<tr>
<th></th>
<th>Group 1</th>
<th>Group 2</th>
<th>Group 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>DELAY (years)</td>
<td>&lt; 3.6</td>
<td>3.6 to 12.4</td>
<td>&gt; 12.4</td>
</tr>
<tr>
<td>Short</td>
<td>medium</td>
<td>long</td>
<td></td>
</tr>
<tr>
<td>RATE (%/ year)</td>
<td>&lt; 1.2</td>
<td>1.2 to 5.2</td>
<td>&gt; 5.2</td>
</tr>
<tr>
<td>Slow</td>
<td>moderate</td>
<td>fast</td>
<td></td>
</tr>
</tbody>
</table>

Of the nine possible trajectory classes, across provinces about 52% belonged to medium delay, normal rate category (Table 2.7). Twenty four percent were medium delay but in the slow (9%) and fast (15%) rate category. Similarly, 17% were medium rate, but had either short or long delay. Very few samples occupied the extreme categories.
Table 2.7 Successional trajectory classification across and within provinces. Numbers are percent of samples.

Across Provinces

<table>
<thead>
<tr>
<th>Delays</th>
<th>Short</th>
<th>Medium</th>
<th>Long</th>
<th>Sum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Slow</td>
<td>0.7</td>
<td>9.4</td>
<td>2.9</td>
<td>13.0</td>
</tr>
<tr>
<td>Moderate</td>
<td>8.7</td>
<td>52.2</td>
<td>8.7</td>
<td>69.6</td>
</tr>
<tr>
<td>Fast</td>
<td>1.4</td>
<td>14.6</td>
<td>1.4</td>
<td>17.4</td>
</tr>
<tr>
<td>Sum</td>
<td>10.8</td>
<td>76.2</td>
<td>13.0</td>
<td>100</td>
</tr>
</tbody>
</table>

WCP

<table>
<thead>
<tr>
<th>Delays</th>
<th>Short</th>
<th>Medium</th>
<th>Long</th>
<th>Sum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Slow</td>
<td>1.1</td>
<td>13.8</td>
<td>3.5</td>
<td>18.4</td>
</tr>
<tr>
<td>Moderate</td>
<td>4.6</td>
<td>60.9</td>
<td>13.8</td>
<td>79.3</td>
</tr>
<tr>
<td>Fast</td>
<td>0</td>
<td>2.3</td>
<td>0</td>
<td>2.3</td>
</tr>
<tr>
<td>Sum</td>
<td>5.7</td>
<td>77.0</td>
<td>17.3</td>
<td>100</td>
</tr>
</tbody>
</table>

CRP

<table>
<thead>
<tr>
<th>Delays</th>
<th>Short</th>
<th>Medium</th>
<th>Long</th>
<th>Sum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Slow</td>
<td>0</td>
<td>2.0</td>
<td>2.0</td>
<td>4.0</td>
</tr>
<tr>
<td>Moderate</td>
<td>15.7</td>
<td>37.2</td>
<td>0</td>
<td>52.9</td>
</tr>
<tr>
<td>Fast</td>
<td>3.9</td>
<td>35.3</td>
<td>3.9</td>
<td>43.1</td>
</tr>
<tr>
<td>Sum</td>
<td>19.6</td>
<td>74.5</td>
<td>5.9</td>
<td>100</td>
</tr>
</tbody>
</table>

The two provinces behaved differently in terms of distribution of the 9 successional trajectory classes. In the WCP about 61% of the sampled stands belonged to the medium delay, normal rate category, compared to only about 37% in the CRP. About 17% of the stands in the WCP had a long delay versus 6% in the CRP. In contrast, the CRP had about 20% in the short delay category versus 6% in the WCP. The most striking
difference was the occurrence of 43% fast and 4% slow rate in the CRP versus the occurrence of 2% fast and 18% slow rate in the WCP.

2.6 DISCUSSION

2.6.1 Multiple Successional Pathways and Rates

Patterns of vegetation change after stand replacement disturbance are affected by the intensity of disturbance, local environmental conditions, and stochastic processes. Therefore, following disturbance, multiple successional pathways are commonly observed (Noble and Slatyer 1980, Abrams, 1985; McCune and Allen 1985) with different rates of recovery highly variable (Myster and Pickett, 1994). Halpern (1988) demonstrated this for six forest communities along a disturbance severity gradient, using ordination techniques on understory communities from two watersheds of the H. J. Andrews Experimental Forest within our study area.

Our results support the theory of multiple successional pathways. Our results also indicate that the patterns of succession were different for the two provinces. We defined succession as a process of changing life forms over time, and we used canopy cover data to represent successional pathways. For simplicity, we described successional pathways using the successional stage at age 50 (Table 2.2), modified by transition states at younger ages. We classified successional pathways into seven different categories (Figure 2.2).
The underlying common trends for both the CRP and WCP were rapid occupation of herbaceous life forms followed by a gradual return to closed canopy recovery (predominantly conifer) on most of the stands. The process of returning to a conifer life form was not the same for all the stands, with a multiplicity of successional pathways being manifested in both the sequence of succession stage change and the rate of change.

Both the photo-interpreted data and modeled data showed that in the CRP a significant proportion of disturbed stands experienced a prolonged period of broadleaf and mixed tree cover, whereas this was uncommon in the WCP. This observation agrees with existing knowledge for these two provinces (Franklin and Dyrness, 1988). The CRP contains both the Sitka Spruce Zone and Western Hemlock Zone, whereas the WCP mainly contains the Western Hemlock Zone only. In the Sitka Spruce Zone, two major kinds of seral forest stands are known to commonly exist: coniferous and hardwood (Franklin and Dyrness, 1988). Broadleaf trees can rapidly occupy disturbed stands (Zavitkovski and Stevens, 1972) and the replacement of broadleaf trees by conifer trees can be a slow process, due to the dense understory in broadleaf stands (Meurisse and Youngberg, 1971). Broadleaf stands are not common in forests of the Western Hemlock Zone even in the CRP, except on very recently disturbed sites or in riparian zones (Franklin and Dyrness, 1988). However, broadleaf lifeforms are known to occur in the riparian zone of both the CRP and WCP. Close
examination of those samples belonging to the CB and CM categories indicated that most occurred within the Sitka Spruce Zone. In the WCP, we also observed that about 3 percent of the sampled stands remained in the SH category and about 22% in the SC category, whereas no sample stands in CRP belongs to these categories.

It has been known for some time that rates of forest succession are variable, yet there have been few remotely sensed studies to document this phenomenon. Successional rate has been interpreted as either the time for recovery to a terminal stage (Major 1974a, Burrows 1990) or as rate of change in vegetation composition (Major 1974b, Prach 1993). For change rates, species turnover and turnover rates have been evaluated by similarity indices (Bornkamm 1981, Donnegan and Rebertus 1999).

We combined both interpretations of successional rate in our analyses. Because we were interested in early forest succession, the terminal stage for our purposes was 70% conifer cover. The derived parameter T70 from the Chapman-Richard’s function represents one interpretation of successional rate. However, instead of using similarities measure for species turnover, we used conifer life-form and canopy cover change rates derived from Chapman-Richards function to describe succession rate (wmRGR, wmAGR, maxRate). In other studies, where succession rates were based on species composition and turnover, species richness and diversity were more strongly emphasized. The use of a
similarity index was more often limited by the available data. Our approach using life-form and canopy cover is more closely related to the biomass aspect of succession and can be easily related to other large scale studies such as carbon modeling. Characterization of succession in this study was based on curve fitting for lifeform and canopy cover data obtained from aerial photo interpretation, which makes it possible to compare data sets for stands of different origin.

Succession, as we defined it, in the CRP was generally faster than in the WCP. The average time required to reach 70% conifer cover for CRP samples was 23 years, which is much shorter than the 42 years for the WCP. Also the rate measurements (wmAGR, wmRGR, maxRate) indicated that the average rate for the CRP was about double that of the WCP (Figure 2.7).

2.6.2 Ecological and Management Implications

Many factors can affect forest succession. Succession rate has been shown to be highly correlated with moisture and/or soil fertility (Olson 1958, Shugart and Heet 1973, Gleeson and Tilman 1990, Prach 1993, Donnegan and Rebertus 1999). In our study area, there is more precipitation in the CRP than in the WCP, and fog and low clouds in the CRP help to alleviate moisture stress for the drier summer period. Soil in the CRP is relative deep, rich, and fine textured compared to soil in the WCP (Franklin and Dyrness 1988). In a subsequent study, we will quantify the relationship
between environmental factors and succession. However, we anticipate finding that variations of successional patterns cannot be explained solely by regional environmental factors such as precipitation and temperature.

In addition to the extreme environmental conditions, biological and management factors are likely also to be important in shaping successional patterns in western Oregon. Besides vegetative competition, below ground processes could be important mechanisms controlling conifer seedling survival and conifer growth. It has been indicated that ectomycorrhizae and subsequent effects were important reforestation aid in western Oregon (Perry et al., 1987). Forest management practices after stand replacement disturbance could affect succession in many different ways including direct reduction of vegetation competition, improved soil nutrition, and more importantly, planting of certain species. However, biological and management related factors are more difficult to measure.

We demonstrated that succession after stand replacement disturbance was highly variable across western Oregon. In our study area, early succession differed in terms of both successional pathway and trajectory. The classification of successional pathway and trajectory, as was developed in this study, should be useful for modeling changes in regional carbon stores over time (Harmon et al., 1996; O'Connell, in prep.).
2.7 CONCLUSIONS

In this study, we evaluated early forest succession by characterizing changes of life forms (shrub/herb, broadleaf tree, conifer tree) and cover using air photos. We defined seven categories of successional pathway, and a set of parameters to describe the successional patterns. Our analysis indicated that successional patterns for the CRP and WCP are different in terms of pathway, rate, and delay factors for conifer cover development.

The method used in this paper allowed for comparison of heterogeneous data sets. The effects of short term fluctuations during succession and a lack of replication were alleviated by treating each sample separately, by means of fitting a trajectory to model the sample data. Quantifying the importance of controlling factors on the succession patterns is a critical next step.
2.8 REFERENCES


Robertson, T. B. 1923. The chemical basis of growth and senescence. Philadelphia and London.


Chapter 3 The Effect of Abiotic Factors on Forest Succession in Western Oregon

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Oregon State University
Corvallis, Oregon
January 12, 2004
3.1 ABSTRACT

In this study, we examined the effect of climatic and physiographic factors on the early phase of forest succession following clearcuts in western Oregon. Succession was defined as the directional change with time of life-form composition of a stand, manifested through changes in canopy cover of different life-forms. The study area consisted of the portions of Coast Ranges Province (CRP) and Western Cascades Province (WCP) that were contained within a Landsat TM scene (path 46, row 29). In total 116 sample stands were examined.

Aerial photos from 1959 to 1997, in roughly 5-year intervals, were interpreted for proportion of conifer cover. Conifer cover change over time was fitted with a Chapman-Richards growth function for each sampled stand, and from these growth curves, parameters of interest related to early forest succession were extracted. These parameters included, for each sample stand, (1) the number of years to reach 5% conifer cover (DELAY), and (2) weighted mean absolute growth rate of conifer cover over the whole growth period (RATE). Both DELAY and RATE showed a wide range of variation over the study area. Many factors could contribute to the variation of DELAY and RATE, including biological, environmental, and management. However, as only environmental factors (climatic and physiographic) were readily available, these were used in correlation and
regression analysis to explore how much of the variation in DELAY and RATE could be explained.

Correlation analysis indicated that among the climatic variables examined, temperature was one of the most important factors influencing both DELAY and RATE both within and across provinces. Precipitation and radiation were less important than temperature. Of all the physiographic variables considered, elevation was the most important one, probably due to its influence of temperature.

Regression analysis explained 23%, 37%, and 29% of the variation in DELAY, and 24%, 25%, and 57% of the variation in RATE, for the WCP, the CRP, and across provinces, respectively. No significant interactions among climatic and physiographic factors were identified for DELAY in the WCP, or for RATE in the CRP. For DELAY in the CRP, the interaction of relative slope position (RSP) and solar radiation (SRAD) were important. Across provinces, the interaction of vapor pressure (VPD) and summer temperature were important for DELAY. For RATE, the interaction of elevation (ELEV) and RSP was important in the WCP, while the interaction of ELEV and SRAD was important in the across provinces analysis.

The variability in succession explained by this study was relatively low. Unexplained variability is likely due to stochastic, biological, and management-related factors, as well as experimental errors associated with characterizing climate variables and successional parameters. Inclusion of
these factors will be important in future research on early forest succession in western Oregon.
INTRODUCTION

Understanding forest succession is critical for forest ecosystem management and biodiversity conservation planning (Knight and Wallace, 1989). In particular, successional pathway and rate have important implications for biogeochemical cycling of nitrogen (Pastor and Post, 1986), and carbon (Botkin and Running, 1984; Harmon, 2001a). Consequently, estimates of successional pathway and rate are important inputs for many ecological models (Hall et al., 1988; Hall, 1991; Harmon et al., 1990; Cohen et al., 1992; O'Connell et al., in prep.).

After stand replacement disturbance in the Pacific Northwest (PNW) region of the United States, forest succession generally leads to a closed canopy conifer condition (Franklin and Dyrness, 1988). However, the rate and density of conifer recovery can vary significantly across the region (Franklin and Hemstrom, 1981; Nesje, 1996; Tappeiner et al., 1997; Poage, 2001). Here, we study early forest succession in western Oregon, focusing on the relationships of two major successional descriptors with various potential controlling abiotic factors.

Succession has many dimensions and has been studied extensively from numerous perspectives (Connell and Slatyer, 1977; Finegan, 1984; Pickett et al., 1987; Halpern, 1988; Glenn-Lewin et al., 1992; Peet, 1992). It is widely recognized that many factors are important contributors to
successional variation, including biotic, abiotic, and management related factors (Turner et al., 1998; Halpern, 2001).

Biotic factors often contribute to forest succession through resource competition (Peterson et al., 1988; Newton and Preest, 1988; Nearty et al., 1990; Farnden, 1994; Stein, 1995; Strothmann and Roy, 1995; Gray and Spies, 1997) and allelopathy (del Moral and Cates, 1971; Mallik, 1987), or indirectly by modifying the environment in a way that is beneficial or detrimental to seedling survival and growth (Coates et al., 1991). Perry et al. (1987, 1989) and Ponge et al. (1998) studied the effects of mycorrhizal fungi on forest regeneration and suggested that below-ground biological mechanisms could strongly affect forest regeneration.

Abiotic factors have also been examined, especially with respect to forest regeneration stocking level. In a study of regeneration within mixed-conifer clearcuts in the Cascades Range, Seidel (1979) found that greater stocking was generally associated with more northerly aspects. Similar patterns were also reported by other researchers (Strothmann, 1979; Minore et al., 1982, and Ferguson et al., 1994). In western Oregon, Nesje (1996) studied the spatial pattern of early forest succession in Lookout Creek Basin, classifying succession into slow, expected, and fast categories. In her analysis, interactions of elevation and aspect, as well as aspect and a topographic convergence index were significant for slow
stands. Interaction of elevation and aspect, and elevation and the topographic convergence index were significant for fast stands.

Management factors include site preparation, planting, and silvicultural practices. Broadcast burning has been a commonly used site preparation technique. This can cause increased moisture stress by exposing seedlings directly to environmental extremes (Minore et al., 1982; Ferguson et al., 1994). Broadcast burning can also influence the persistence of mycorrhizal fungi (Parke et al., 1984; and Amaranthus and Perry, 1989). Axelrood et al. (1998) reported that planting of seedlings with poor vigor is more likely to lead to regeneration failures.

Most of the above-mentioned studies of forest succession were based on choronosequences or relatively short periods of observations involving small areas, and results among these studies were inconsistent. In a previous study of early successional patterns in western Oregon, we used historical aerial photos for samples stands from a portion of Siuslaw National Forest and Willamette National Forest contained within a single Landsat Thematic Mapper (TM) image. The succession process studied here includes both natural and human influenced succession process. Although the majority of disturbed stands that we studied returned to closed conifer condition within 50 years, a wide range of successional pathways and rates were observed. Thus, we defined succession as the temporal directional change of life-form composition, as manifested through changes
in canopy cover of different life-forms. Successional pathways were classified into 7 categories that could be characterized by two descriptors: DELAY (time to reach 5% conifer cover) and RATE (weighted mean absolute growth rate), defined as the mean rate of conifer cover accumulation (Yang et al., in prep.). In the current study, we examined potential controlling factors on these two descriptors.

In this study, it was not practical to quantify biotic influences over the large area studied. Additionally detailed information about management treatments was not available for many of the stands studied. Thus, we examined how much of the variation observed in forest succession could be accounted for by readily available spatial databases containing abiotic factor information. The objective was therefore to examine effects of abiotic factors and their interactions on DELAY and RATE. The factors studied were primarily climatic and physiographic variables.

3.3 METHODS

3.3.1 Study Area

The area studied was the portions of the Coast Ranges Province (CRP) and the Western Cascades Province (WCP) of western Oregon contained in Landsat TM path/row 46/29 (Figure 3.1). Because the availability of historical aerial photos varies, but is most extensive over National Forest lands, stands from the Siuslaw National Forest in CRP and Willamette National Forest in WCP were studied.
In general, the PNW region has a maritime climate of warm, dry summers and mild, wet winters, which exhibits a strong gradient with changes in latitude, longitude, and elevation. These climatic conditions favor growth of evergreen life-forms, except in riparian areas where broadleaf trees may dominate. Upslope forests have a ratio of coniferous to broadleaf trees of 1000:1 in this region (Kuchler, 1964), and have among
the greatest biomass accumulations and highest productivity levels of any ecosystem on earth (Waring and Franklin, 1979). Besides conifer and broadleaf trees, many shrub and herbaceous species exist in the study area (Frankin and Dyrness, 1988).

The CRP is characterized by mild temperature with prolonged cloudy periods. Average temperatures range from 5 °C in January to 16 °C in July, and the mean annual precipitation is 3000mm. Depending on location, summers range from cool to warm and elevations range from 450 to 750m. Sedimentary rock types are typical in the CRP. Two primary forest zones include the Sitka Spruce Zone and the Western Hemlock Zone (Franklin and Dyrness, 1988).

The climate of the WCP is also maritime with mild, wet winters and warm, dry summers. Average temperatures range from -5 °C in January to 23 °C in July and annual precipitation averages about 2300mm. Elevations range from 450 to 3100m, with volcanic rocks dominating most of the area. The province consists primarily of the Western Hemlock Zone (Franklin and Dyrness, 1988).

### 3.3.2 Successional Descriptors

In Yang et al. (see Chapter 2), changes in percent cover of different life-forms were observed from historical aerial photos for 138 randomly selected 1-ha plots in the CRP and the WCP. With these data, a Chapman-Richards growth function was used to model observed cover changes.
Based on this growth function, two derived parameters: DELAY and RATE (Table 3.1), were used to characterize successional trajectories for each plot. Of the 138 sample plots, 22 were removed from the current analysis due to an insufficient number of temporal data points to adequately fit the Chapman-Richards growth function. This yielded a total of 116 sample plots. For the Chapman-Richards growth function, 

\[ f(t) = 100 \times (1 - e^{-kt})^b \]

\( f(t) \) is the canopy cover at time \( t \), \( b \) describes the shape of the fitted curve, and \( k \) is a rate constant.

Table 3.1 Successional descriptor variables.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Formula</th>
<th>Detail</th>
</tr>
</thead>
<tbody>
<tr>
<td>DELAY</td>
<td>( \frac{-\ln(1 - 0.05^{1/b})}{k} )</td>
<td>Time to reach 5% cover</td>
</tr>
<tr>
<td>RATE</td>
<td>( \frac{A \times k}{2 \times (b + 2)} )</td>
<td>Weighted mean absolute growth rate</td>
</tr>
</tbody>
</table>

### 3.3.3 Controlling factors

Precipitation, temperature, radiation, and vapor pressure data for sample plots were extracted from the Daymet U.S. database, an 18 year (1980-1997) 1-km resolution daily data set (Thornton et al., 1997, 1999, 2000). From the daily data, mean (TDAY), maximum (TMAX), and minimum (TMIN) daily temperature, mean number of frost days per year (FROSTDAY), mean daily precipitation (PRCP), mean number of no-rain days per year (NORAIN), mean daily potential solar radiation (SRAD), and
Table 3.2 Codes and definitions of climatic and physiographic controlling factors considered.

<table>
<thead>
<tr>
<th>Code</th>
<th>Units</th>
<th>Description</th>
</tr>
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<tbody>
<tr>
<td><strong>Climate Factors</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Temperature</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TDAY</td>
<td>°C</td>
<td>Mean daily temperature</td>
</tr>
<tr>
<td>TMAX</td>
<td>°C</td>
<td>Mean daily maximum temperature</td>
</tr>
<tr>
<td>TMIN</td>
<td>°C</td>
<td>Mean daily minimum temperature</td>
</tr>
<tr>
<td>FROSTDAY</td>
<td>days</td>
<td>Mean number of days with minimum temperature below 0°C in one year</td>
</tr>
<tr>
<td>SMRTMP</td>
<td>°C</td>
<td>Mean daily temperature in May – September</td>
</tr>
<tr>
<td>WTRTMP</td>
<td>°C</td>
<td>Mean daily temperature in November – March</td>
</tr>
<tr>
<td><strong>Precipitation</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PRCP</td>
<td>cm</td>
<td>Mean daily precipitation</td>
</tr>
<tr>
<td>NORAIN</td>
<td>days</td>
<td>Mean number of days without any precipitation in one year</td>
</tr>
<tr>
<td>SMRPRCP</td>
<td>cm</td>
<td>Mean daily precipitation in May – September</td>
</tr>
<tr>
<td>WTRPRCP</td>
<td>cm</td>
<td>Mean daily precipitation in November – March</td>
</tr>
<tr>
<td>SMRTSMRP</td>
<td>°C/cm</td>
<td>Moisture stress during the growing season, SMRTMP/SMRPRE</td>
</tr>
<tr>
<td>CONTPRE</td>
<td>%</td>
<td>Mean percentage of annual precipitation falling in June-August</td>
</tr>
<tr>
<td><strong>Radiation</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SRAD</td>
<td>W/m²</td>
<td>Mean daily potential solar radiation</td>
</tr>
<tr>
<td>VPD</td>
<td>Pa</td>
<td>Mean daily water vapor pressure</td>
</tr>
<tr>
<td><strong>Physiographic Factors</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ELEV</td>
<td>m</td>
<td>Elevation</td>
</tr>
<tr>
<td>SLOPE</td>
<td>%</td>
<td>Slope</td>
</tr>
<tr>
<td>TRANSASP</td>
<td>-</td>
<td>cos(45-aspect)+1</td>
</tr>
<tr>
<td>SOUTHNESS</td>
<td>-</td>
<td>cos(aspect + 180)</td>
</tr>
<tr>
<td>EASTNESS</td>
<td>-</td>
<td>sin(aspect)</td>
</tr>
<tr>
<td>RSP</td>
<td>-</td>
<td>Relative slope position</td>
</tr>
<tr>
<td>TRMI</td>
<td>-</td>
<td>Topographic relative moisture index</td>
</tr>
</tbody>
</table>
mean daily vapor pressure (VPD) were derived. Ohmann and Spies (1998) demonstrated the importance of regional climate conditions during the growing season and the cool season for woody plant community distribution. Thus, we also derived mean summer (SMRTMP) and winter (WRTTMP) daily temperature, mean summer (SMRPRCP) and winter (WTRPRCP) daily precipitation, summer moisture stress (SMRTSMRP) and summer precipitation concentration (CONTPRE) from the daily Daymet data.

All physiographic data (Table 3.2) were derived from the USGS 10-m digital elevation model (DEM) dataset and represent estimates of the mean values for each 1-ha plot. Several physiographic variables were derived. Elevation (ELEV) and slope (SLOPE) were derived as simple averages. Aspect (compass direction of slope) was transformed by trigonometric functions (Beers et al., 1966; Roberts, 1986) into TRANSASP, SOUTHNESS, and EASTNESS. These transformations convert the more standard measure of aspect into measurements of exposure. Relative slope position (RSP) was calculated as an index of a plot's position relative to the top and bottom of the slope. RSP affects both the general thermal and hydrologic regime of a site. Topographic relative moisture index (TRMI) (Parker, 1982) values were computed from slope steepness, topographic position, and slope configuration (convex to concave). TRMI theoretically increases with soil moisture by assuming that on steep slopes or ridgetops,
the soil is shallow and therefore limited in moisture capacity. As slope decreases and topographic position moves down the slope, accumulated drainage area and soil moisture increase.

3.3.4 Data Analysis

Preliminary analysis revealed non-linearity in the relationships of RATE and DELAY with the potential controlling factors. Thus, RATE and DELAY were log-transformed to linearize the relationships. Pearson correlation coefficients were used to explore the relationships of DELAY and RATE with individual potential controlling factors. This analysis was conducted both within the WCP and CRP, and across provinces to explore if there were provincial-level effects controlling succession. For plotting purposes, simple least squares regression models were derived for each variables and its relationship with both DELAY and RATE.

We also evaluated the interactions of controlling variables. Given that some of the variables in Table 3.2 were highly correlated, not all of the variables listed were significant in the presence of other variables. Therefore, using the correlation matrix of the potential controlling factors on RATE and DELAY, we identified and used only the most uncorrelated variables that represent temperature, precipitation, radiation, and physiography. These included TMIN, SMRTMP, SMRPRCP, CONTPRE, SRAD, VPD, ELEV, SLOPE, RSP, SOUTHNESS, EASTNESS, and TRMI. All selected variables were standardized by subtracting the mean value to
reduce multicollinearity (Aiken and West, 1991), before being subjected to a stepwise regression. Even though a log transformation was conducted to linearize the relationships, exploratory analysis revealed that quadratic relationships were more appropriate for DELAY with TMIN and ELEV. Therefore, quadratic terms for TMIN and ELEV were also included. The significance levels for entering and leaving the model were 0.10 and 0.05, respectively. However, when a variable was used as part of an interaction term, it was always included as a main effect regardless of the p-value (Aiken and West, 1991). All statistical analyses were done in SAS (SAS Institute, 1999). Statistical results were judged as not significant (p > 0.05), significant (0.01 < p ≤ 0.05), or highly significant (p ≤ 0.01).

3.4 RESULTS

3.4.1 General Correlation Patterns
The correlations of DELAY and RATE with the potential controlling variables were generally low, with only about 25% of the correlations larger than 0.35 (Table 3.3). For both DELAY and RATE in the CRP, most of the correlations considered were not significant, and the highest correlations were 0.35 and -0.39, respectively. About one-half of the correlations for both DELAY and RATE in the WCP were significant. The highest correlations were -0.41 for both successional descriptors. Results across provinces were similar to those of the WCP for DELAY. However, for RATE, several correlation values were greater than 0.50.
Table 3.3 Correlation coefficients for the relationships of DELAY and RATE with potential controlling factors

<table>
<thead>
<tr>
<th>Climate</th>
<th>Temperature</th>
<th>CRP</th>
<th>WCP</th>
<th>Across Provinces</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Ln(DELAY)</td>
<td>Ln(RATE)</td>
<td>Ln(DELAY)</td>
</tr>
<tr>
<td>TDAY</td>
<td>0.22</td>
<td>0.13</td>
<td>-0.37**</td>
<td>0.38**</td>
</tr>
<tr>
<td>TMAX</td>
<td>0.27</td>
<td>0.15</td>
<td>-0.35**</td>
<td>0.38**</td>
</tr>
<tr>
<td>TMIN</td>
<td>0.04</td>
<td>0.06</td>
<td>-0.41**</td>
<td>0.37**</td>
</tr>
<tr>
<td>FROSTDAY</td>
<td>-0.03</td>
<td>0.01</td>
<td>0.39**</td>
<td>-0.39**</td>
</tr>
<tr>
<td>SMRTMP</td>
<td>0.35*</td>
<td>0.19</td>
<td>-0.34**</td>
<td>0.36**</td>
</tr>
<tr>
<td>WTRTMP</td>
<td>0.04</td>
<td>0.04</td>
<td>-0.39**</td>
<td>0.40**</td>
</tr>
<tr>
<td>Precipitation</td>
<td>PRCP</td>
<td>-0.01</td>
<td>-0.01</td>
<td>0.34**</td>
</tr>
<tr>
<td></td>
<td>NORAIN</td>
<td>-0.09</td>
<td>-0.02</td>
<td>-0.21</td>
</tr>
<tr>
<td></td>
<td>SMRPRCP</td>
<td>-0.08</td>
<td>-0.08</td>
<td>0.26*</td>
</tr>
<tr>
<td></td>
<td>WTRPRCP</td>
<td>0.01</td>
<td>0.02</td>
<td>0.35**</td>
</tr>
<tr>
<td></td>
<td>SMRTSMRP</td>
<td>0.15</td>
<td>0.10</td>
<td>-0.34**</td>
</tr>
<tr>
<td></td>
<td>CONTPRE</td>
<td>-0.23</td>
<td>-0.19</td>
<td>-0.13</td>
</tr>
<tr>
<td>Radiation</td>
<td>SRAD</td>
<td>-0.16</td>
<td>-0.28</td>
<td>0.03</td>
</tr>
<tr>
<td></td>
<td>VPD</td>
<td>0.31</td>
<td>0.15</td>
<td>-0.31**</td>
</tr>
<tr>
<td>Physiography</td>
<td>ELEV</td>
<td>-0.02</td>
<td>-0.13</td>
<td>0.33**</td>
</tr>
<tr>
<td></td>
<td>SLOPE</td>
<td>0.19</td>
<td>-0.35*</td>
<td>-0.18</td>
</tr>
<tr>
<td></td>
<td>RSP</td>
<td>0.13</td>
<td>-0.07</td>
<td>-0.17</td>
</tr>
<tr>
<td></td>
<td>SOUTHERNESS</td>
<td>-0.13</td>
<td>-0.31*</td>
<td>0.11</td>
</tr>
<tr>
<td></td>
<td>EASTNESS</td>
<td>0.06</td>
<td>-0.39*</td>
<td>-0.16</td>
</tr>
<tr>
<td></td>
<td>TRANSASAP</td>
<td>0.14</td>
<td>-0.15</td>
<td>-0.17</td>
</tr>
<tr>
<td></td>
<td>TRMI</td>
<td>0.10</td>
<td>0.29</td>
<td>0.10</td>
</tr>
</tbody>
</table>

** P ≤ 0.01; * P ≤ 0.05
DELAY decreased and RATE increased with an increase in all the temperature variables except FROSTDAY both in the WCP and across provinces analysis (signs in Table 3.3). No obvious patterns existed for precipitation and radiation variables. ELEV was the most important physiographic variable considered (Table 3.3).

Compared to the CRP, there generally was considerable more variation in the controlling factors within the WCP (Figure 3.2-3.9). As such, across province patterns were mainly influenced by patterns in the WCP. Furthermore, in some cases (e.g. DELAY with TDAY and TMAX), relationships were opposite for the two provinces. However, in these cases and others, across province relationships were a function of the difference between the provinces.

In general, for the WCP and across provinces, both DELAY and RATE showed similar relationships with the potential controlling variables studied. The notable exceptions were precipitation (PRCP, NORAIN, WTRPRCP, and CONTPRE) and radiation (VPD) variables, where relationship for the WCP and across provinces were opposite for both DELAY and RATE.

The WCP and CRP responded to the controlling factors differently (Table 3.3). With regard to temperature, both DELAY and RATE showed stronger correlation with temperature variables (|r|=0.34-0.41) in WCP than CRP. Only SMRTMP (r=0.35) was significantly correlated with DELAY and
Figure 3.2 Scatter plots of DELAY and temperature variables. Dotted and solid lines indicate least squares fittings for across and within provinces, respectively. See Table 3.3 for correlation coefficients and significance levels. Circles and squares represent samples from WCP and CRP, respectively.
Figure 3.3 Scatter plots of RATE and temperature variables. Dotted and solid lines indicate least squares fittings for across and within provinces, respectively. See Table 3.3 for correlation coefficients and significance levels. Circles and squares represent samples from WCP and CRP, respectively.
Figure 3.4 Scatter plots of DELAY and precipitation variables. Dotted and solid lines indicate least squares fittings for across and within provinces, respectively. See Table 3.3 for correlation coefficients and significance levels. Circles and squares represent samples from WCP and CRP, respectively.
Figure 3.5 Scatter plots of RATE and precipitation variables. Dotted and solid lines indicate least squares fittings for across and within provinces, respectively. See Table 3.3 for correlation coefficients and significance levels. Circles and squares represent samples from WCP and CRP, respectively.
Figure 3.6 Scatter plots of DELAY and radiation variables. Dotted and solid lines indicate least squares fittings for across and within provinces, respectively. See Table 3.3 for correlation coefficients and significance levels. Circles and squares represent samples from WCP and CRP, respectively.

Figure 3.7 Scatter plots of RATE and radiation variables. Dotted and solid lines indicate least squares fittings for across and within provinces, respectively. See Table 3.3 for correlation coefficients and significance levels. Circles and squares represent samples from WCP and CRP, respectively.
Figure 3.8 Scatter plots of DELAY and physiographic variables. Dotted and solid lines indicate least squares fittings for across and within provinces, respectively. See Table 3.3 for correlation coefficients and significance levels. Circles and squares represent samples from WCP and CRP, respectively.
Figure 3.9 Scatter plots of RATE and physiographic variables. Dotted and solid lines indicate least squares fittings for across and within provinces, respectively. See Table 3.3 for correlation coefficients and significance levels. Circles and squares represent samples from WCP and CRP, respectively.
all other correlations were either not significant or very weak ($r \leq 0.27$) in the CRP. In addition, DELAY in the WCP was negatively correlated with SMRTMP, while in CRP these were positively correlated.

With regard to precipitation, DELAY generally increased and RATE decreased with an increase in precipitation in WCP. However, DELAY and RATE did not respond significantly to precipitation in the CRP.

For radiation, DELAY decreased with an increase in VPD in the WCP ($r=-0.31$), while it increased ($r=0.31$) with increasing VPD in the CRP. In contrast, RATE increased in an increase in VPD in the WCP ($r=0.33$), but VPD did not have much influence on RATE in the CRP ($r=0.15$).

Most of the physiographic variables studied were not important except ELEV for the WCP. However, RATE in CRP was negatively correlated with slope (SLOPE, $r=-0.35$) and aspect (SOUTHNESS, $r=-0.31$; EASTNESS, $r=-0.39$). No physiographic factors were important for DELAY in CRP ($|r| < 0.20$).

### 3.4.2 Regression Models

The models for both DELAY and RATE in WCP and CRP were all weak ($r^2 = 0.23-0.37$) and no precipitation factors were included in the final models (Table 3.4).

With respect to DELAY, only temperature (TMIN) and physiographic variables (SOUTHNESS and TRMI) were included in the final model for WCP (Table 3.4B). No interactions were important for the WCP. For the
CRP, in addition to temperature (SMRTMP) and radiation (SRAD), the interaction of SRAD and RSP were also significant (Table 3.4A).

With respect to RATE, for the WCP, only physiographic variables (ELEV and RSP) were included in the model (Table 3.5B). The interaction of ELEV and RSP was also significant. No climatic variables were in the final model. For the CRP, only physiographic variables (SLOPE and SOUTHNESS) were included, but no interactions were important and no climatic variables were included (Table 3.5A).

The across province model for DELAY was also weak ($r^2 = 0.29$), but the model for RATE was much stronger ($r^2 = 0.57$) (Table 3.4c and Table 3.5c). No precipitation factors were included in the models for DELAY and RATE. For DELAY, only temperature (TMIN and SMRTMP) and radiation (VPD) were included. Interaction of SMRTMP and VPD was also significant, and a quadratic term for TMIN was included. For RATE, all of the main effects included were physiographic variables (ELEV and TRMI). The interaction of ELEV and radiation (SRAD) was important, but SRAD was not significant in the model as a main effect.

3.5 DISCUSSION

We studied the influence of various climatic and physiographic factors on delay of conifer recovery (DELAY) and rate of conifer canopy accumulation (RATE) after stand replacement disturbance. Results indicated that only a small proportion of variability in DELAY and RATE can
Table 3.4 Results of stepwise regression for DELAY

**A. CRP \((R^2 = 0.37)\)**

*Analysis of Variance*

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>Sum of Squares</th>
<th>Mean Square</th>
<th>F Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model</td>
<td>4</td>
<td>3.0686</td>
<td>0.7672</td>
<td>5.1050</td>
</tr>
<tr>
<td>Error</td>
<td>35</td>
<td>5.2596</td>
<td>0.1503</td>
<td>Prob &gt; F</td>
</tr>
<tr>
<td>C. Total</td>
<td>39</td>
<td>8.3283</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Parameter Estimates*

| Term      | Estimate | Std Error | t Ratio | Prob>|t| |
|-----------|----------|-----------|---------|------|
| Intercept | 1.8129   | 0.0618    | 29.34   | <.0001|
| SMRTMP    | 0.3971   | 0.1089    | 3.65    | 0.0009|
| SRAD      | -0.0247  | 0.0116    | -2.12   | 0.0409|
| RSP       | 0.0016   | 0.0057    | 0.29    | 0.7772|
| RSP*SRAD  | -0.0027  | 0.0009    | -2.98   | 0.0052|

**B. WCP \((R^2 = 0.23)\)**

*Analysis of Variance*

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>Sum of Squares</th>
<th>Mean Square</th>
<th>F Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model</td>
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<td>1.3857</td>
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<tr>
<td>Error</td>
<td>72</td>
<td>14.1098</td>
<td>0.1960</td>
<td>Prob &gt; F</td>
</tr>
<tr>
<td>C. Total</td>
<td>75</td>
<td>18.2671</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Parameter Estimates*

| Term      | Estimate | Std Error | t Ratio | Prob>|t| |
|-----------|----------|-----------|---------|------|
| Intercept | 2.0831   | 0.0508    | 41.02   | <.0001|
| TMIN      | -0.1708  | 0.0457    | -3.74   | 0.0004|
| SOUTHNESS | 0.2563   | 0.1135    | 2.26    | 0.0269|
| TRMI      | 0.0231   | 0.0102    | 2.25    | 0.0274|

**C. Across provinces \((R^2 = 0.29)\)**

*Analysis of Variance*

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>Sum of Squares</th>
<th>Mean Square</th>
<th>F Ratio</th>
</tr>
</thead>
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<td>1.6971</td>
<td>9.1642</td>
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<tr>
<td>Error</td>
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<td>20.3707</td>
<td>0.1852</td>
<td>Prob &gt; F</td>
</tr>
<tr>
<td>C. Total</td>
<td>115</td>
<td>28.8562</td>
<td></td>
<td>&lt;.0001</td>
</tr>
</tbody>
</table>

*Parameter Estimates*

| Term      | Estimate | Std Error | t Ratio | Prob>|t| |
|-----------|----------|-----------|---------|------|
| Intercept | 1.7007   | 0.1166    | 14.58   | <.0001|
| TMIN      | -0.4644  | 0.1277    | -3.64   | 0.0004|
| SMRTMP    | 1.0459   | 0.3717    | 2.81    | 0.0058|
| VPD       | -0.0117  | 0.0047    | -2.50   | 0.0141|
| TMIN*TMIN | 0.0815   | 0.0234    | 3.48    | 0.0007|
| VPD*SMRTMP| -0.0009  | 0.0004    | -2.08   | 0.0395|
Table 3.5 Results of stepwise regression for RATE.

### A. CRP ($R^2=0.25$)

#### Analysis of Variance

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>Sum of Squares</th>
<th>Mean Square</th>
<th>F Ratio</th>
</tr>
</thead>
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<td>Error</td>
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<tr>
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<td>0.0046</td>
</tr>
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</table>

#### Parameter Estimates

| Term              | Estimate | Std Error | t Ratio | Prob>|t|
|-------------------|----------|-----------|---------|------|
| Intercept         | 1.5582   | 0.0547    | 28.51   | <.0001 |
| SLOPE             | -0.0216  | 0.0078    | -2.76   | 0.0090 |
| SOUTHNESS         | -0.2439  | 0.0966    | -2.53   | 0.0159 |

### B. WCP ($R^2=0.24$)

#### Analysis of Variance

<table>
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<tr>
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#### Parameter Estimates

| Term              | Estimate | Std Error | t Ratio | Prob>|t|
|-------------------|----------|-----------|---------|------|
| Intercept         | 0.6219   | 0.0569    | 10.88   | <.0001 |
| ELEV              | -0.0010  | 0.0002    | -4.17   | <.0001 |
| RSP               | -0.0073  | 0.0039    | -1.85   | 0.0683 |
| ELEV*RSP          | 0.00003  | 0.00002   | 2.06    | 0.0430 |

### C. Across provinces ($R^2=0.57$)

#### Analysis of Variance

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>Sum of Squares</th>
<th>Mean Square</th>
<th>F Ratio</th>
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</tbody>
</table>

#### Parameter Estimates

| Term              | Estimate | Std Error | t Ratio | Prob>|t|
|-------------------|----------|-----------|---------|------|
| Intercept         | 0.86611  | 0.050095  | 17.29   | <.0001 |
| ELEV              | -0.001177| 0.000129  | -9.12   | <.0001 |
| TRMI              | 0.0189563| 0.006572  | 2.88    | 0.0047 |
| SRAD              | -0.000618| 0.004662  | -0.13   | 0.8947 |
| ELEV*SRAD         | 0.0000255| 0.000011  | 2.39    | 0.0185 |
be accounted for by the climatic and physiographic factors both within and across provinces \((r^2=0.23-0.37)\). One notable exception was for RATE across provinces \((r^2=0.57)\).

Patterns across provinces were mainly dominated by patterns in the WCP, with a few exceptions. For most of the factors studied, the WCP and CRP had different ranges with the WCP expressing more variation. Therefore, in most cases, patterns across provinces were dominated by patterns within the WCP. For those exceptions, for example Figure 3.5a and 3.7b, both the WCP and CRP showed the same trend along environmental gradients, but across provinces there were an opposite trend. In general, the controlling factors had less influence in CRP than in WCP.

### 3.5.1 Influence of Climate

The literature suggested that temperature is probably the most important environmental factor influencing seedling survival and growth in PNW. Many biochemical and physiological processes are directly influenced by temperature (Raven and Curtis, 1970; Lavender, 1990; Sutton 1991). Temperature regime, especially extreme temperatures, had great influence on seedling survival and growth (Cui and Smith, 1991; Farnden, 1994). Water deficiency has been reported to occur with low soil temperature (Goldstein et al., 1985; Carter et al., 1988), even when soil moisture was not limiting (Farnden, 1994). In addition to reducing water flow
through the soil-plant-air continuum, low temperature, especially early in the
growing season, can also limit root and shoot growth and mineral and water
uptake (Lavender and Overton, 1972; Halverson and Emmingham, 1982;
Farnden, 1994). This in turn reduces tree growth during the whole growing
season. Frost is one of the most critical factors affecting seedling survival
and early growth (Stathers, 1989; Butt, 1990; Steen et al., 1990; Farnden,
1994). While extreme low temperature has the potential to cause mortality,
high summer temperature can also cause problems for seedling survival
and growth (Cochran, 1969; Heninger and White, 1974; Stathers, 1989),
especially on south aspects.

The temperature variables examined in this study could be classified
into three general groups representing average (T DAY), low (TMIN,
WTRTMP, and FROSTDAY), and high (TMAX and SMRTMP) temperature
for a stands. Our results indicated that temperature was the most
influencing climatic factor for development of conifer cover. Low
temperature variables were more closely associated with DELAY in WCP,
while high temperature variables had more influential effects on DELAY in
CRP. The main reason for this phenomenon is that the temperature
regimes for WCP and CRP are different. Generally, CRP has higher
temperature than WCP (Figure 3.2), resulting in different extreme
temperature conditions for WCP and CRP. Through those possible
mechanisms described above, effects of low temperature were more
evident in WCP, while effects of high temperature were more evident in CRP. This suggests that to reduce the DELAY length and to enhance seedling survival and growth, different planting seasons may be necessary for WCP and CRP. Fall planting would be more appropriate for CRP, while spring planting would be more appropriate for WCP.

Temperature did not exhibit the same effects on RATE as on DELAY. For both the WCP and CRP, RATE increased with increasing temperature (Table 3.3, Figure 3.3). This was not unexpected. In this study, RATE was represented by weighted mean absolute growth rate (Table 3.1). Since less weight was given to growth rate during the early period, the growth rate especially during the delay period has less influence on RATE. Therefore, the influence of extreme temperature was minimized in RATE. This also suggested that extreme temperatures were less likely to exert influence on established seedlings. After the delay period, established seedlings were able to deal with extreme temperature conditions more successfully, and increased temperature generally results in more active physiological processes, hence increased growth rate.

Generally, even though precipitation has an important influence on vegetation distribution, it is not a limiting factor for DELAY and RATE in the studied region. The effects of radiation are exerted mainly through controlling other important factors for establishment and growth of trees such as air and soil temperature, precipitation, and soil moisture.
Correlation analysis revealed that there were trends of increasing DELAY and decreasing RATE with increasing precipitation (Figure 3.4 and 3.5). The exact reason for this pattern is unclear, but we think this might be due to several factors. First, precipitation was not a limiting factor for DELAY and RATE. Second, the correlation results may have been confounded by other more important factors. For example, increased precipitation would increase soil water content, which in turn affects soil warming due to the high volumetric heat capacity of water (Stather and Spittlehouse, 1990), resulting in cold soil.

Weather conditions during planting and immediately after planting may also be important contributors to successional variation, especially for DELAY. It has been suggested that most mortality occurred during the first growing season, and much of this is probably caused by extreme environmental conditions. However, in this study, due to lack of detailed information about planting season for the sample stands, these more time specific variables could not be used in this study.

3.5.2 Influence of Physiography

It is known that forest regeneration is slower for high elevation stands than low elevation stands. In the PNW, forest regeneration is generally less successful as elevation increases (Strothmann, 1979; Minore and Dubrasich, 1981) with the exception of southern and warmer sites (Halverson and Emmingham, 1982). The main effect of elevation is
manifested through the decreasing gradient of temperature associated with increasing elevation. The cooler temperatures and shorter growing seasons associated with higher elevation were reflected in forest growth, with slower growth at higher elevation. In addition to the effects on plant physiological processes through the temperature regime, the decreasing daily average temperature with increased elevation may also result in spring-time delay of plant development (Ogilvie, 1969), which in turn affects the overall growth rate. Even though there were no strong patterns for DELAY and RATE in the CRP, we did observe that DELAY increased and RATE decreased with increasing elevation for WCP and across provinces. This agrees with the observation that effects of elevations are manifested through effects on temperature regime.

Slope and aspect interacted with each other to affect stand radiation and temperature. On south aspects, steeper slopes would increase the radiation interception, while on north facing slopes, interception is dramatically decreased. The direct effects of aspect and slopes have implications not only for temperature, but indirect effect on ecosystem processes such as photosynthesis and moisture regimes. Since south aspects have more incoming solar radiation, sites with southern aspects will have earlier reduction in soil moisture contents resulting in improved conditions for soil warming. However, extreme high surface temperature is more likely on south-facing slopes, especially for low elevation stands. It
has been reported that conifer establishment following harvest is often more
difficult to ensure on south- and west-facing slopes than on north- and east-
facing slopes (Seidel 1979; Strothmann 1979; Graham et al. 1982; Minore
et al. 1982; Ferguson et al. 1994).

In this study, neither slope nor aspect was significantly correlated
with succession except for RATE in CRP (Table 3.3). Conifer cover
accumulation was slower on south facing slopes than north facing slopes in
CRP. Even though aspect was not a significant contributor in WCP, the
regression model for DELAY indicated that together with TMIN and TRMI,
aspect (SOUTHNESS) was also significant.

Soil moisture is the key to tree growth and development, as virtually
every aspect of plant morphology and physiology is highly correlated with
soil water stress (Zahner, 1968; Kramer and Boyer, 1995). In this study,
TRMI was used as a surrogate for soil moisture content and results
indicated that RATE increased with TRMI in the WCP and CRP, but not for
across provinces.

3.5.3 Degree of Variations Explained

The regression models developed in this study explained: 37% of the
variability in DELAY and 25% of the variability in RATE for CRP; 23% of the
variability in DELAY and 24% of the variability in RATE for WCP; 29% of
the variability in DELAY and 57% of the variability in RATE across
provinces.
The large proportion of unexplained variability could be caused by numerous factors, including stochastic factors, and lack of explanatory information. Several factors related to successional descriptors and potential controlling factors may also have resulted in variability that could not be explained. These include errors from photo interpretation, imperfect fitting of the Chapman-Richards growth function, errors in the Daymet database, and errors in the DEM data.

A large amount of variability in vegetation recovery is caused by stochastic factors (Franklin et al., 1985; Vitousek and Walker, 1987; Halpern and Franklin, 1990; del Moral and Bliss, 1993). These include temperature variation right after planting, natural seed regeneration from the surrounding forest, etc. All these factors could influence forest succession in the study area.

Perhaps equally, or more important are variations caused by biotic and management related factors, which were not included in this study. Biotic interference or enhancement, site preparation, planting techniques, planting season, and condition of planted seedlings are all important factors influencing conifer development. These factors constitute unaccounted source of errors in our analysis.

*Biotic factors*

Competition from associated vegetation has a significant influence on seedling survival and growth (e.g., Newton and Preest 1988; Coates et
al. 1991; Farnden 1994; Whitehead and Harper 1998). Above-ground, competition can occur for growing space and light, while below-ground, competition can occur for soil moisture and nutrients (Haeussler and Coates 1986). Severe competition can lead to death or suppressed growth for unsuccessful competitors. However, associated vegetation does not always exert negative effects on seedling survival and growth. The vegetation of a site can also facilitate seedling survival by protecting seedlings from either frost or excessive solar radiation, by adding soil organic matter and nutrients, or by stabilizing soil on steep slopes, especially in extreme environments (Farnden 1994).

Mycorrhizal fungi play an important role in the establishment and survival of tree seedlings (Amaranthus and Perry, 1987). Mycorrhizal fungi enhance nutrient and water uptake while increasing disease resistance for the host plants. Absence of mycorrhizal fungi from where they used to exist (for example, caused by death after forest clearcut) may lead to depletion in nutrients, organic matter, water holding capacity and physical structure (Perry et al. 1989). Detailed information on the effects of mycorrhiza fungi can be found in Wright and Tarrant (1958), Parke (1982), Rose (1983), Parke et al. (1984), Amaranthus et al. (1989), Read (1991), Mallik (2003).

Interaction with animals can also be important in seedling survival. Grazing from herbivores can offset tree growth, but can also cause seedling mortality (Stein 1995). Gashwiler (1971) found that insect damage can
cause significant seedling mortality in the H. J. Andrews Experimental Forest in western Oregon.

It is unlikely that the biotic factors described above would have caused the same effects on DELAY and RATE. We hypothesize that the effects of mycorrhizal fungi would be more evident on DELAY and effects of vegetative competition would be more evident on RATE. The negative effects of animal damage will have more effect on DELAY than on RATE, while damage from insects could affect both DELAY and RATE.

Management factors

Site preparation, planting and stand management practices can have significant effects on seedling survival and growth. Historically, in the PNW, broadcast burning is usually applied to logging slash to reduce fire hazard, to facilitate planting, and to reduce competition from shrub species. However, reduced fuel loading reduces future organic matter and nitrogen input to the burned stand, resulting in greater soil instability. In addition, intensive burning also exposes newly planted seedlings directly to environmental extremes, which may result in seedling mortality due to increased moisture stress (Ferguson et al. 1994). Broadcast burning can also influence the persistence of mycorrhizal fungi on disturbed stands. Wright and Tarrant (1958), Parke et al. (1984), and Amaranthus et al. (1989) suggested that mycorrhizal fungi in burned clearcuts (and
particularly in severely burned sites) can be greatly reduced relative to undisturbed or unburned soils.

The physiological condition of planted seedlings directly affects their survival. Sites planted with poor seedlings are more likely to have regeneration failures (Axelrood et al. 1998). In addition, planting time during the year can also have negative or positive effects on seedling survival (Strothmann, 1979).

For some planted stands, thinning and fertilization may be applied to improve tree growth. Fertilization can improve site quality by adding a new source of nutrients to the soil. Thinning is a common silvicultural practice which removes some trees within a stand to provide more growing space for the remaining trees. All these management related factors would contribute to the variation in DELAY and RATE.

In general, we expect most of these management-related factors have more influence on DELAY than on RATE, except thinning and fertilization. Factors such as site preparation, planting time etc. have influence on seedling survival, hence DELAY.

3.6 CONCLUSIONS

No simple regression model can fully explain the variation in forest succession in western Oregon. In this study, only a small proportion of variation in DELAY (time to reach 5% canopy cover) and RATE (weighted mean absolute growth rate over the entry growing period) of early
secondary forest succession could be explained by climatic and physiographic factors. We hypothesize that the unexplained variation was mainly due to stochastic, biotic, and management factors. To investigate controlling factors for early forest succession, including biotic and management factors would help to understand succession processes. Research on the effects of controlling factors through a more mechanistic model could give more insight on early forest successional process.

The length of delay tends to be longer in severe environmental conditions, especially extreme temperature. The controlling effects of climatic and physiographic factors were different for WCP and CRP. In part, this was caused by the fact that the WCP and CRP occupy different regions along an environmental gradient. DELAY in the WCP was influenced more by low temperature than by high temperature, while DELAY in the CRP was influenced more by high temperature than by low temperature. This has some important silviculture implications. For example, to reduce the DELAY for forest succession, spring planting is more appropriate for WCP, while fall planting is more appropriate for CRP.
3.7 REFERENCES


Chapter 4 Conclusions

The research reported in this dissertation examined forest succession from the perspective of changing life forms after stand replacement disturbance. In this research, I sought to accomplish two tasks: (1) characterize the patterns of forest succession in western Oregon; and (2) examine the relative importance of various climatic and physiographic factors on the observed patterns of forest succession.

I studied forest succession from the perspective of changing life-forms instead of the traditional species composition change. For the purpose of characterizing successional patterns, seven early forest successional pathways were defined in this study. I developed a new approach to characterize successional patterns based on photo-interpretation and modeling with a Chapman-Richards growth function. This new approach makes it possible to compare data sets for stands of different origin and to analyze data more robustly when there are no replicates.

Results from photo-interpretation and canopy cover modeling indicated that forest succession after stand replacement disturbance varied greatly across the region studied.

I compared successional patterns in the WCP with those in the CRP using derived parameters from the Chapman-Richards growth function. The CRP and WCP not only differed in successional pathways, but also in term of successional rates. With respect to successional pathways, it is more
likely for a stand to return to closed broadleaf forest conditions in the CRP than in the WCP, whereas shrub and semi-closed pathways were more common in the WCP than in the CRP. Conifer regeneration in the WCP generally had a longer delay and lower rate of development, compared to the CRP.

These findings regarding the successional pathways and trajectories have important implications for other ecological research. An average rate of forest succession is commonly assumed in landscape modeling. From the perspective of carbon dynamics, a faster succession rate is more beneficial, as it can quickly offset losses of carbon from decomposition. However, I have demonstrated that there exists a wide range of rates and pathways over a region. Harmon (2001b) has demonstrated that during secondary succession total carbon stores usually decrease for some time until increases in the live pool can offset the losses from the detritus and soils pools. Figure 4.1 shows ranges in total carbon store dynamics using 5 hypothetical scenarios for the CC pathway with different rates of conifer accumulation. Given this range, regional carbon dynamics could be directly influenced by patterns of live biomass change after stand replacement disturbance. Successional pathways developed in this study can be used to estimate the potential amount of biomass, while successional rate can be used to estimate the rate of live biomass changes. The results from this
study can be linked with a regional carbon store modeling framework, such as STANDCARB (Harmon et al., 1996).

The implications of the findings in this study for biodiversity conservation are different from carbon dynamics. Large variation in successional pathways and rates is more likely to enhance biodiversity than a homogeneous succession pattern. Different successional pathways and rates after stand replacement disturbance would create a more heterogeneous landscape, which could theoretically maintain more species.
To understand controls on early forest succession processes, I examined the relationships of climatic and physiographic factors with the successional descriptors: DELAY and RATE. Correlation analysis indicated that temperature was one of the most important factors for both DELAY and RATE. In general, conifer cover accumulation was faster with higher temperature. However, temperature effects in the CRP and WCP were different for DELAY. DELAY in the CRP increases with temperature, especially at high temperature, whereas in the WCP, DELAY decreases with an increase in temperature, especially at low temperature. Precipitation and radiation were not as important explanatory factors as temperature.

Of all the physiographic factors considered, elevation was the most important. All other physiographic factors did not have a major influence on forest succession, in terms of DELAY and RATE. The influences of physiographic factors were probably through their influence on temperature, and possibly through effects on soil moisture.

The variability explained by climatic and physiographic factors was relatively low. Regression analysis explained 23%, 37%, and 29% of the variation in DELAY, and 24%, 25%, and 57% of the variation in RATE, for the WCP, the CRP, and across provinces analysis, respectively. No interactions among climatic and physiographic factors were found for DELAY in the WCP, or RATE in the CRP. For DELAY, relative slope position (RSP) and solar radiation (SRAD) interacted in the CRP, vapor
pressure (VPD) and summer temperature interacted in across provinces. For RATE, elevation (ELEV) and RSP interacted in the WCP, while ELEV and SRAD interacted across provinces. The unexplained variability could be caused by data quality in photo-interpretation and statistical derivation of successional descriptors. Stochastic, biological, and management related factors are also likely important for the unexplained variation.

There are several logical extensions of this study. The relations established in this study for DELAY and RATE with climate and physiography were not very strong except for RATE across provinces. The models developed in this study may have limited application in regional and landscape modeling directly, but from this study we confirmed that forest succession after stand replacement disturbance is a variable and complex process. No simple model can adequately explain variations in forest succession. The controlling effects appeared to be more localized over the landscape. Future study on forest succession should focus more on the biotic and management-related factors.

The models developed in this study, while they indicate reasonable controls, may not be very useful for prediction purposes. To provide useful information for regional and landscape modeling, it may be better to make observations directly. Aerial photos are valuable source of information for observing forest succession, but these photos are not always available over the entire landscape and have infrequent intervals. In addition, photo
interpretation is a very time consuming process. In this study, forest succession was interpreted as a change in life-forms manifested through canopy cover changes, which have also been monitored successfully by satellite remote sensing technology (Cohen et al., 1998; Woodcock et al., 2001). Hence, we suggest that successional processes could be more efficiently observed over the landscape with satellite-based remote sensing. For example, examining spectral trajectories from historical MSS, Landsat TM, and ETM+ data could be used to help monitoring early forest succession and provide knowledge about forest succession over the landscape.

The findings from this study are important for understanding early forest succession in western Oregon. More importantly, they suggest some opportunities for further research. The suggestions listed are only a few that I will pursue in the future.


Mallik, A. U. 2003. Conifer regeneration problems in boreal and temperate forests with ericaceous understory: role of disturbance, seedbed limitation,


Robertson, T. B. 1923. The chemical basis of growth and senescence. Philadelphia and London.


Thornton, P. E., H. Hasenauer, and M. A. White. 2000. Simultaneous estimation of daily solar radiation and humidity from observed temperature


