Modeling early forest succession following clear-cutting in western Oregon

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Abstract: In the Pacific Northwest, the process of conifer development after stand-replacing disturbance has important implications for many forest processes (e.g., carbon storage, nutrient cycling, and biodiversity). This paper examines conifer development in the Coast Range Province and Western Cascades Province of Oregon using repeat interpretation of historic aerial photographs from 1959 to 1997 to examine the canopy cover change of different life forms: shrubs, hardwood trees, and conifer trees. Ninety-four stands from the Western Cascades Province and 59 stands from the Coast Range Province were photointerpreted 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 the Chapman–Richards function, these stands were classified into one of seven early forest successional trajectories defined by the vegetation physiognomy. Succession in the Coast Range Province and Western Cascades Province were compared using 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; however, our results also indicate that early forest succession differs in the two study regions in terms of both trajectories and rates. Conifer regeneration in the Western Cascades Province tends to have longer delays in establishing and slower rates compared with the Coast Range Province.

Résumé : Dans le nord-ouest des États-Unis, le processus de développement des conifères à la suite d'une perturbation menant au remplacement du peuplement affecte grandement plusieurs processus forestiers (p. ex., l'entreposage du carbone, le recyclage des nutriments et la biodiversité). Cette étude se déroule dans deux régions de l'Oregon : la chaîne côtière et les Cascades occidentales, et porte sur le développement de conifères évalué à partir de l'interprétation répétée de photographies aériennes prises entre 1959 et 1997 dans le but d'observer les changements dans la couverture de la canopée de différentes formes végétales : des arbustes, des arbres caducifoliés et des résineux. Quatre-vingt quatorze peuplements des Cascades occidentales et 59 peuplements de la chaîne côtière ont été photo-interprétés à des intervalles d'environ cinq ans. Une fonction de croissance de type Chapman-Richards a été utilisée pour modéliser le développement du couvert de conifères pour chacun des peuplements échantillonnés. En se basant sur les données photographiques et sur la fonction de Chapman–Richards, ces peuplements ont été classifiés selon sept trajectoires de succession forestière juvénile déterminées par la physionomie de la végétation. Les successions de la chaîne côtière et des Cascades occidentales ont été comparées en utilisant les paramètres dérivés de la fonction de Chapman-Richards. Le taux et la densité de la régénération de conifères variaient grandement selon la station, ce qui corrobore les résultats provenant d'études précédentes. Cependant, les résultats des auteurs indiquent aussi que la succession forestière juvénile diffère selon la région étudiée en termes de trajectoire et de taux. La régénération de conifères des Cascades occidentales tend à avoir de plus longs délais d'établissement et de plus faibles taux que ceux de la chaîne côtière.

[Traduit par la Rédaction]

Introduction

There is 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).

In the Pacific Northwest region of the United States, the order of likely vegetation transitions at a site is generally predictable, with larger growth forms replacing smaller ones (e.g., shrubs replacing herbaceous plants and trees replacing

Received 27 August 2004. Accepted 14 June 2005. Published on the NRC Research Press Web site at http://cjfr.nrc.ca on 2 September 2005.

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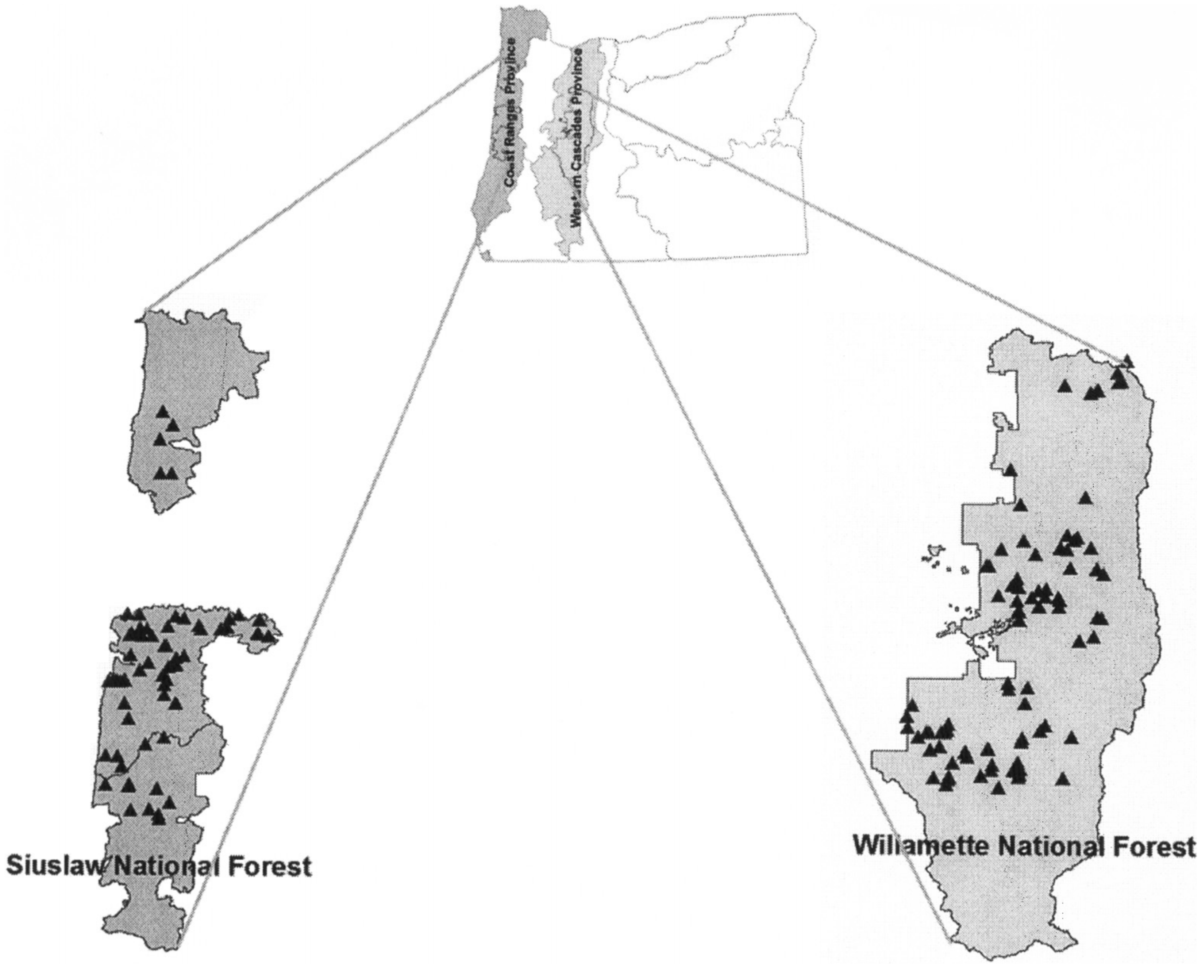
 doi: 10.1139/X05-132

Fig. 1. Study area. The triangles indicate the location of photointerpreted plots.



shrubs). However, the rates and specific trajectories of succession can vary considerably among sites (Tappeiner et al. 1997; Winter 2000). 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 dominance. Other stands might go rapidly and directly from shrub condition to conifer dominance (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 present (Perry et al. 1989). Using aerial photographs, Nesje (1996) indicated that the development of conifer dominance varied considerably after stand-replacing disturbance in the H.J. Andrews Experimental Forest. However, no study has been done to quantify the early forest successional rate in a larger area.

In this paper, we studied early forest succession in western Oregon focusing on conifer cover development after clearcutting. Early forest succession was defined as temporal change of forest stand composition and vegetation physiognomy from clear-cut to closed-canopy forest. We used interpretations of aerial photos from 1959 to 1997 to examine secondary forest succession after stand-replacing disturbance in terms of canopy cover change of different life forms: shrubs, hardwood trees, and conifer trees. The main objectives for this study were to: (*i*) characterize alternative early-successional trajectories among harvested stands in western Oregon, (*ii*) develop a method for quantifying rate of succession and characterizing differences in successional trajectory and rate, and (*iii*) compare early forest successional rates between the Coast Range Province and Western Cascades Province (Fig. 1).

Materials and methods

Study area

The study area is the Coast Range Province and Western Cascades Province of western Oregon (Fig. 1). Since the availability of historical aerial photos varied, but was most extensive over National Forest lands, stands from the Siuslaw National Forest in the Coast Range Province and Willamette National Forest in the Western Cascades Province were used.

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 (Waring and Franklin 1979). The climate exhibits a strong gradient with changes of latitude, longitude, and elevation.

The Coast Range Province is characterized by mild temperature with prolonged cloudy periods. Average temperatures range from 5 °C in January to 16 °C in July. Annual precipitation is about 3000 mm. Depending on location, sum-

Table 1. Historical aerial photos used for repeat photointerpretation.

Western Cascades Province			Coast Range Province		
Year	Scale	Format	Year	Scale	Format
1959	1 : 12 000	BW	1961–1962	1 : 12 000	True color
1967	1 : 15 840	BW	1968–1969	1 : 15 840	True color
1972	1 : 15 840	True color	1972	1 : 15 840	True color
1979	1 : 12 000	True color	1979	1 : 12 000	True color
1988	1 : 40 000	BW	1984	1 : 12 000	True color
1990	1 : 12 000	True color	1989	1 : 12 000	True color
1997	1 : 12 000	True color	1993–1995	1 : 12 000	True color

Note: BW, black and white.

mers in the Coast Range Province range from cool to warm. Elevations generally vary from 450 to 750 m. The climate of the Western Cascades Province is also maritime with mild, wet winters and warm, dry summers. Average temperatures range from –5 °C in January to 23 °C in July. Annual precipitation in the Western Cascades Province is about 2300 mm, and elevations vary from 450 to 3100 m.

Geologic conditions differ in the Coast Range Province and Western Cascades Province. Sedimentary rock types are typical of the Coast Range Province, while the volcanic rocks dominate most of the Western Cascades Province. Forest soils vary in the two regions, reflecting the variation in parent materials and topography (Franklin and Dyrness 1988).

Vegetation

In contrast with other moist and mesic regions in the world where hardwood species typically dominate, Pacific Northwest forests have a ratio of coniferous to hardwood trees of 1000:1 (Kuchler 1964). Moreover, forests in the Pacific Northwest are characterized as having among the greatest biomass accumulations and some of the highest forest productivity levels on earth (Waring and Franklin 1979). However, the productive potential is higher in the Coast Range Province than in the Western Cascades Province. Two major forest vegetation zones exist in the study area (Franklin and Dyrness 1988). The Coast Range Province includes vegetation of the Sitka spruce zone and the western hemlock zone, whereas the Western Cascades Province includes vegetation 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.

Forest management practices usually varied among ownerships. Since the sampling areas in this study are both on federal land, the management practices were most likely similar. For the majority of stands, clear-cutting was the cause of stand-replacing disturbance. Broadcast burning was usually applied to logging slash to reduce fire hazard, facilitate planting, and reduce competition from shrub species. Planting is commonly used in the two study areas for managed forest, and occasionally partial harvest is performed on managed stands in national forest.

Data acquisition

Previous studies indicated that elevation and aspect interact to affect conifer development in the H.J. Andrews Experimental Forest (Nesje 1996), one of the most studied forests in the region. To apply this knowledge of topographic controls, we classified the study area into eight aspect classes (45° intervals, starting at 0° (north)) and six elevation classes (300-m intervals) taken from a 25-m digital elevation model (DEM) that was resampled from a 30-m DEM. Facets with less than 36 DEM cells (2.25 ha) were removed from the potential sample area. This ensured that the final samples had at least a 25-m 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 stands (1 ha each). Of these, 94 were selected from the Western Cascades Province, and 59 were selected from the Coast Range Province based on the availability of aerial photographs. Most of the aerial photos used were true color having various scales (Table 1).

By repeated photointerpretation, the percent cover in 5% intervals of conifer trees, hardwood trees, shrub and (or) grass, and open condition was determined for each 1-ha sample stand and each photo year. For samples in the Western Cascades Province, stand origin dates were obtained from the VEGIS database (Willamette National Forest 2001). For samples in the Coast Range Province, origin dates were obtained from the VEGE GIS coverage (Siuslaw National Forest 1992).

Fitting vegetation cover growth curves

The stand origin and duration of photointerpreted period varied among sample stands in the study area. Differences in dates of stand origin and periods of repeat air photos necessitated normalization of the photointerpretation data to facilitate direct comparison among stands within and among provinces. To normalize the photointerpreted 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 and Holland 1919; Robertson 1923), and Chapman–Richards (Causton et al. 1978; see Richards 1969 for an extensive review of various growth functions). We chose the Chapman–Richards function, because that function accommodates the wide variety of growth curves that existed in our data. A Chapman–Richards function (Richards 1959; Hunt 1982; Ratkowsky 1990) has the form of

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

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. Since canopy cover was estimated from air photos with 5% intervals, the asymptotical maxi-

Table 2. Definitions of successional stages.

Code	Name	% tree cover	% conifer or % hardwood	Definition
OP	Open	0	na	Usually the initial stage after stand-replacing disturbance
SH	Shrub and herb	<30	Variable	Tree cover is less than 30%
SC	Semiclosed	30–70	Variable	Tree cover is between 30% and 70%
CC (I, II)	Closed conifer	>70	Conifer >70%	Total tree cover is greater than 70% with more than 70% of tree cover being conifer; I or II indicates stand condition during the SC stage (see text)
CH (I, II)	Closed hardwood	>70	Hardwood >70%	Total tree cover is greater than 70% with more than 70% of tree cover being hardwood; I or II indicates stand condition during the SC stage (see text)
CM	Closed mixed	>70	70%> conifer >30% or 70%> hardwood >30%	Total tree cover is greater than 70%; both hardwood and conifer tree are within the range of 30%–70% of total tree cover

Note: na, not applicable.

mum canopy cover was considered to be 100%, although in theory it could be as low as 96%. The initial percent canopy cover for clear-cut stands were considered to be zero. Therefore, a simplified function was used to model canopy cover change for each sample stand:

$$[2] \qquad f(t) = 100(1 - e^{-kt})^b$$

Numerous age-class descriptions have been applied to Pacific Northwest forest (Cohen et al. 1995; Boyd et al. 2002; Franklin et al. 2002). In this study, forests less than 50 years old were considered as early-successional forests (Jiang et al. 2004). Since the actual maximum age for photointerpreted stands was close to 50 years, this was a natural maximum in this study. Percent cover as a function of time since stand origin (up to 50 years) was modeled separately for each sample stand using SAS (SAS Institute Inc. 1999). The parameters of each stand growth function were defined for percent conifer cover and for percent tree cover, combining conifers and hardwoods, and represented as a unique trajectory.

Successional trajectories

The successional pathway after stand-replacing disturbance was defined here as the shift over time in vegetation community from ephemeral herbaceous life forms, to taller perennial shrubs, to hardwood trees, conifer trees, or a mixture of the two (Franklin and Dyrness 1988; Perry et al. 1989). The process of vegetation community shifting is influenced by both natural forest regeneration and human activities such as planting and stand management. Different classification schemes have been used in forest structural condition classification in terms of canopy cover (Cohen et al. 1995; O'Neil et al. 2001). For this study, several successional stages were defined in terms of canopy cover (Table 2). The transition time between different successional stages varied because of differences in rate of canopy cover accumulation, which resulted in different early forest successional trajectories. The open stage occurs immediately after stand-replacing disturbance, at which time grasses and herbaceous plants quickly occupy a site. The open stage transitions to the shrub and herb stage, which lasts until tree cover reaches 30%, at which time it is defined as being in a semiclosed stage. During the semiclosed stage, the dominant life form can switch between conifer, hardwood, and a mixture of the two. At the time of canopy closure (defined as 70% or greater tree cover), a stand will be dominated by conifer trees (closed conifer stage), hardwood trees (closed hardwood stage), or in a mixed condition (closed mixed stage). If a closed conifer stand was mixed or dominated by hardwood trees when in the semiclosed stage, its trajectory is designated CC II (closed conifer). If dominated by conifer in semiclosed stage, then it is designated CC I. Conversely, if a closed hardwood stand was mixed or dominated by conifers during the semiclosed stage, its trajectory is designated CH II (closed hardwood); otherwise it is designated CH I. Stands reaching the closed mixed stage may have been in mixed or pure-tree condition during the semiclosed stage, and in that case the trajectory is designated CM. For a stand still in semiclosed stage at age 50, its trajectory is designated SC. Similarily if a stand is in shrub and herb stage at age 50, its trajectory is designated SH.

The boundary conditions for defining seven basic categories of an early forest successional trajectory are shown in Fig. 2. Stands following the SH trajectory do not reach 30% tree cover within 50 years after disturbance (lower curve, Fig. 2*a*). Similarly, stands following the SC trajectory have total tree cover between 30% and 70% at age 50 (upper curve, Fig. 2*a*). In both Figs. 2*b* and 2*c*, the top curves represent total tree canopy cover. The lower curve in Fig. 2*b* represents 30% of the top curve, and the lower curve in Fig. 2*c* represents 70% of the top curve. In both Figs. 2*b* and 2*c*, the areas under the lower curve represent the proportion of hardwood cover.

To precisely describe the successional trajectories for the sampled stands, the actual photointerpretation 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 photointerpretation data, as these were the most accurate information readily available. As not all sample stands had reached 50 years since disturbance, the modeled successional stages at age 50 were used as the final reference stage for cross-stand comparisons.

Successional rates

In this study, successional rate represents how fast tree cover increased over time. Together with life form, succession rate determines the successional stage at any point in time. As such, successional trajectories for stands following the same

Fig. 2. Boundary conditions for successional trajectory categories. (*a*) Shrub trajectory has tree cover under 30%, and semiclosed trajectory has tree cover under 70%; (*b*) total tree cover is at least 70%, and conifer is dominant life form; (*c*) total tree cover is at least 70%, and hardwood is the dominant life form; (*d*) total tree cover is at least 70%, and conifer and hardwood are the co-dominant life forms.

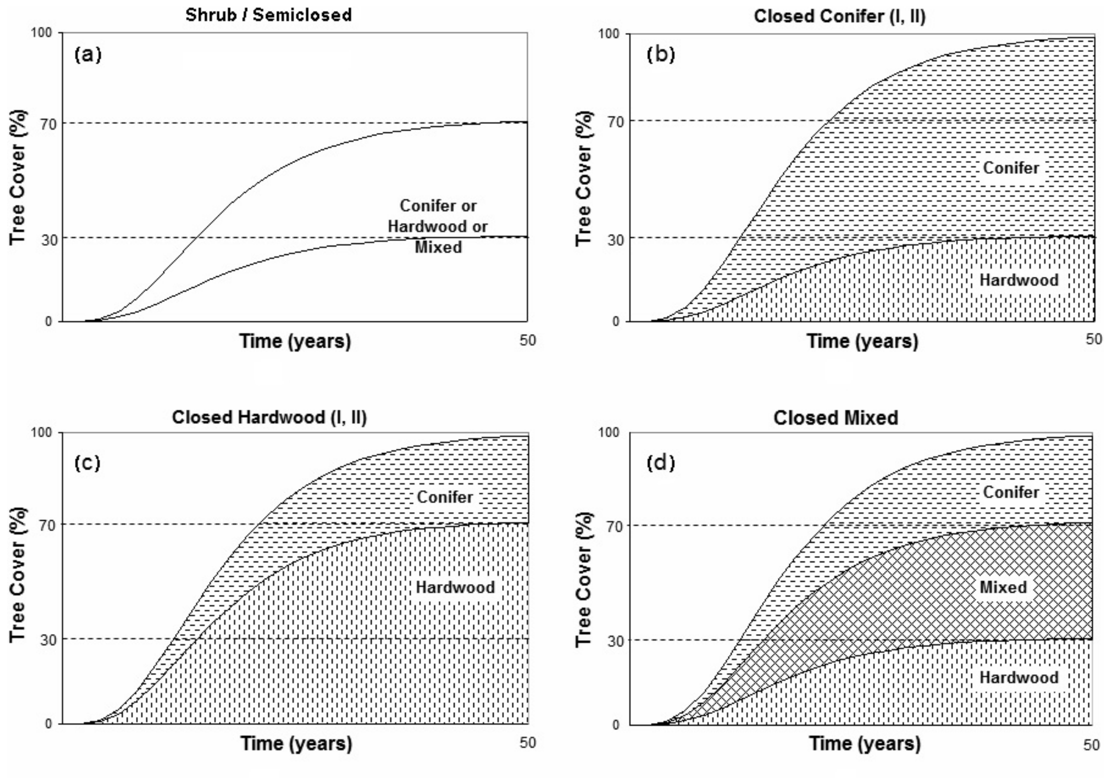


Table 3. Parameters used to describe successional rate.

Parameter	Formula	Detail
DELAY	$-\dfrac{\ln(1-0.05^{1/b})}{k}$	Time to reach 5% cover
wmRGR	$-\dfrac{k}{b-1}$	Weighted mean relative growth rate
wmAGR	$-\dfrac{Ak}{2(b+2)}$	Weighted mean absolute growth rate
MaxRate	$Ak\left(1-\dfrac{1}{b}\right)^{b-1}$	Maximum absolute growth rate
TmaxRate	$-\dfrac{\ln b}{k}$	Time to reach maximum absolute growth rate
T70	$-\dfrac{\ln(1-0.7^{1/b})}{k}$	Time to reach 70% cover
AGP	T70 – DELAY	Active growth period

pathway may differ because of differences in successional rate. Since parameters 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 eq. 2. Thus, to characterize the variation in successional rates and compare rates between the Coast Range Province and Western Cascades Province, several parameters were derived from the Chapman–Richards function (Table 3) (Richard 1959; Causton and Venus 1981). DELAY is defined as the time to reach 5% conifer canopy cover, which can be used to indicate whether stagnation has occurred after stand-replacing disturbance. Weighted mean relative growth rate (wmRGR) and weighted mean absolute growth rate (wmAGR) are used to characterize the overall conifer canopy development rate over the entire growth period. The maximum absolute growth rate (MaxRate) represents the potential maximum conifer canopy development rate. More detailed discussion about the biological significance of these parameters is presented by Richards (1959). In addition to the above three direct measures of rate, we added three time-associated parameters that indirectly characterize succession rate. As conifer canopy development rate eventually decreases with time, TmaxRate represents how quickly a stand will reach its MaxRate. The parameter T70 represents the time to reach closed conifer forest (70% cover), and AGP is the active growth period, the period in which conifer cover is continuously increasing.

Since the rate of 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 the Coast Range Province and Western Cascades Province, the density distribution of the parameters from Table 3 were derived using S-plus (Insight-

Fig. 3. Scatter plots of conifer cover over time from the Coast Range Province (left) and Western Cascades Province (right). The lines indicate the upper and lower envelope of the data cloud for the two sample areas formed by linking the extreme stand data.

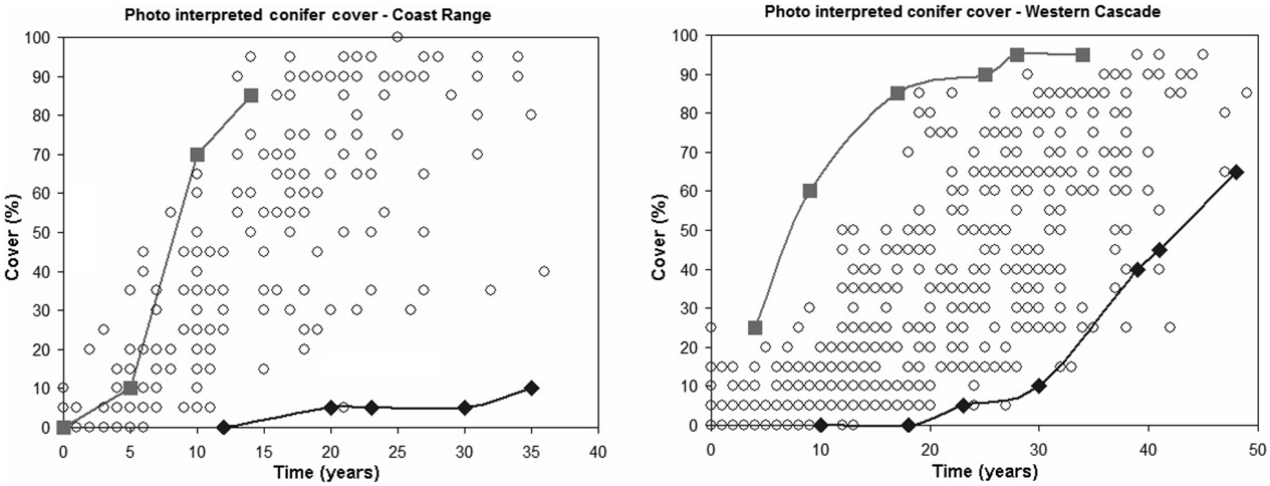
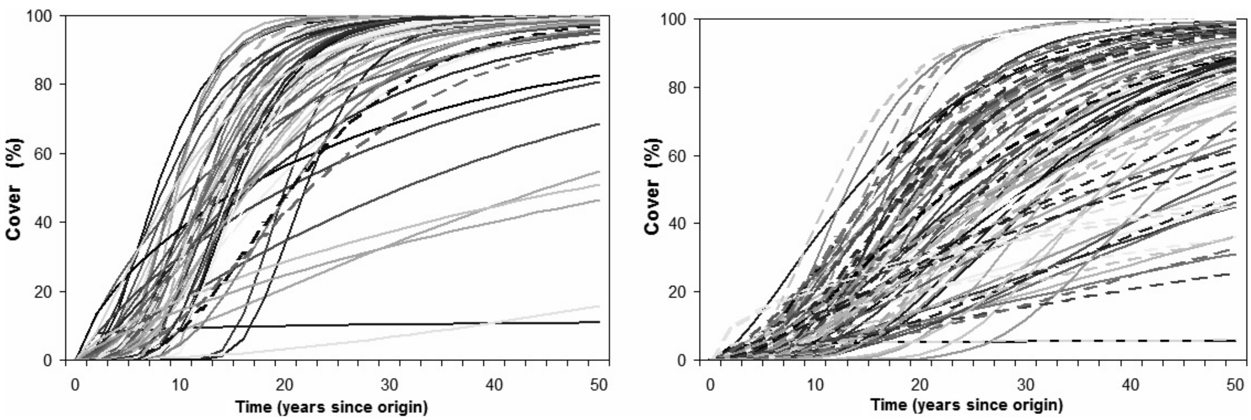


Fig. 4. Modeled conifer cover trajectories for the Coast Range Province (left) and Western Cascades Province (right). Each curve represents the cover trajectory for the first 50 years after stand-replacing disturbance using the developed Chapman–Richards growth function.



ful Corporation 2001). The two regions were also compared in terms of these parameters using a Student's *t* test.

Results

General patterns of succession

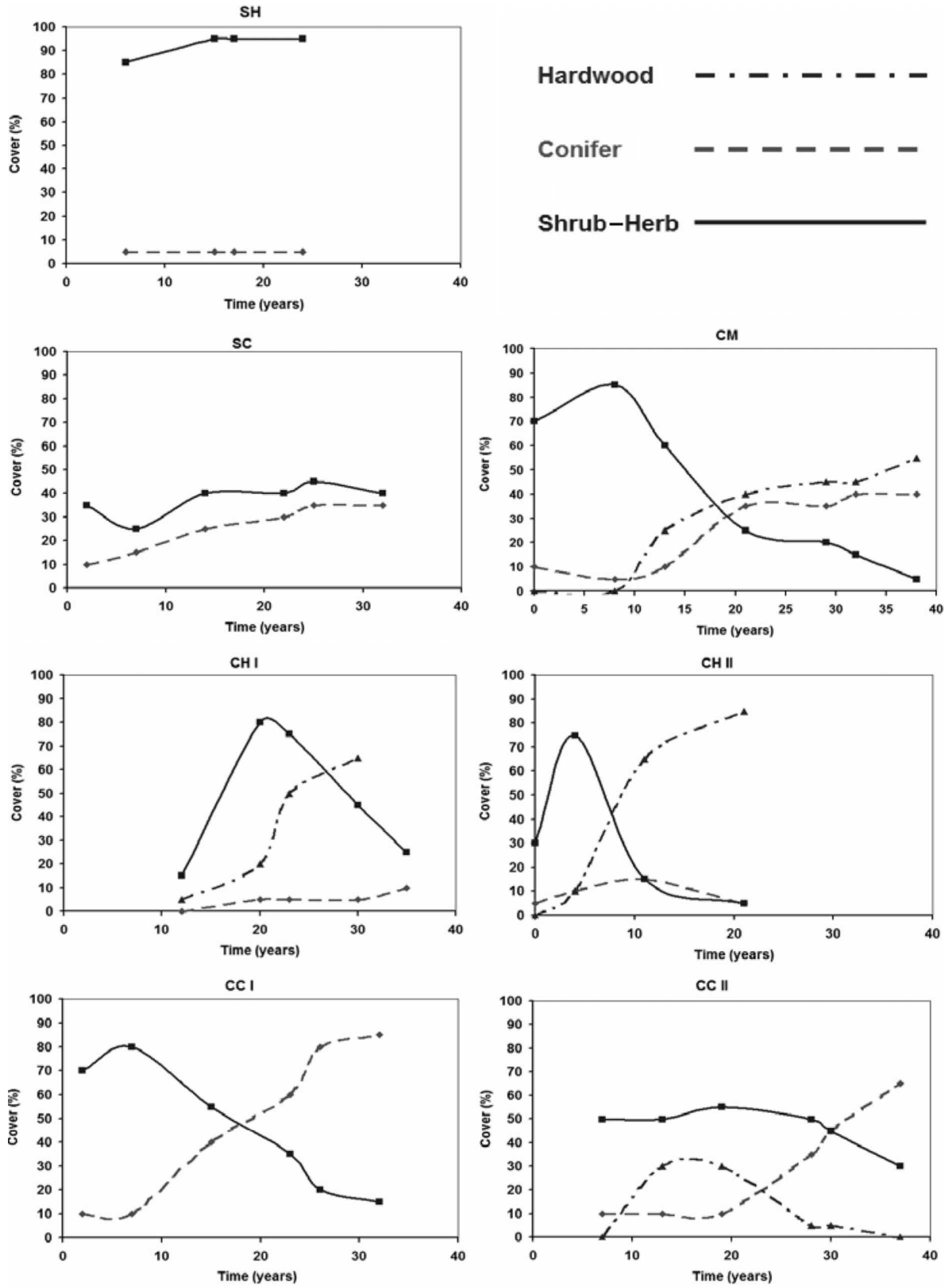
Scatter plots (Fig. 3) and modeled conifer cover (Fig. 4) over time indicate that there was a wide range of conifer cover accumulation patterns over time among stands. This confirms that conifer accumulation over time is highly variable among stands and showed that conifer cover accumulation for stands in the Coast Range Province was generally faster than in the Western Cascades Province. In addition, stands varied with respect to when accumulation of conifer cover begins to accelerate. Once a stand had reached 5% canopy cover, it generally showed a rapid increase in canopy cover (Fig. 4).

Successional trajectories

Photointerpretation revealed that in both the Coast Range Province and Western Cascades Province, herbaceous vegetation quickly occupied a site immediately after stand-replacing disturbance, although much of the herb cover was eventually replaced by trees. Examples of actual successional trajectories based on photointerpretation data are shown in Fig. 5. Analysis indicated that by age 50, the majority of sampled stands returned to closed conifer stage in both provinces (CC I and CC II in Fig. 6). However, in the Western Cascades Province, over 25% of stands had not returned to a closed tree canopy condition, whereas in the Coast Range Province, all sampled stands returned to a closed tree canopy condition. In the Coast Range Province, nearly 7% of the sampled stands returned to a closed-canopy hardwood condition (CH I and CH II), and about 8% returned to a closed mixed condition (CM). In the Western Cascades Province, there were no sample stands that became closed hardwood stands, but approximately 3% returned to a mixed forest condition.

These results indicate that disturbed forest stands return more quickly to closed tree condition in the Coast Range Province than in the Western Cascades Province. However, hardwood trees were more likely to occur during early succession in the Coast Range Province than in the Western Cascades Province. The results also indicate the existence of stands in Western Cascades Province that may be returning to closed conditions very slowly (SH and SC in Fig. 7).

Fig. 5. Examples of different successional trajectories. Each figure represents a stand type, showing the cover of different life forms that existed on the stand over the photointerpretation periods. SH, shrub and (or) herb; SC, semiclosed; CM, closed mixed; CH I, closed hardwood I; CH II, closed hardwood II; CC I, closed confier I; CC II, closed conifer II.



Successional rates

Based on the modeled growth curves (Fig. 4), the distribution of successional rates varied both within and across provinces (Fig. 8). In general the time needed for conifer establishment and dominance in the Western Cascades Province was longer than the Coast Range Province. The variability of each parameter was of the same magnitude in both provinces (Table 4); however, each parameter had a significantly different distribution in each province. Sample stands in the Western Cascades Province had longer DELAY than the Coast Range Province. On average, reaching conifer cover of 5% in stands was delayed about 7 years in the Coast Range Province, while it was delayed about 9 years in the Western Cascades Province (Table 4). Weighted mean relative growth rate (wmRGR), weighted mean absolute growth rate (wmAGR), and maximum absolute growth rate (MaxRate) had similar distributions both across provinces and within a province (Fig. 8). Student's t tests indicated that the means of all three parameters for conifer accumulation were significantly different (Table 4) between the Western Cascades Province and Coast Range Province. For the Coast Range Province, wmAGR was more than twice that for stands in the Western Cascades Province (4.8 vs. 2.3). Similar relationships existed between wmRGR and MaxRate for the Western Cas-

Fig. 6. Successional trajectory distribution for the Coast Range Province and the Western Cascades Province. The number indicates the proportion of stands belonging to each successional trajectory. SH, shrub and (or) herb; SC, semiclosed; CM, closed mixed; CH I, closed hardwood I; CH II, closed hardwood II; CC I, closed confier I; CC II, closed conifer II.

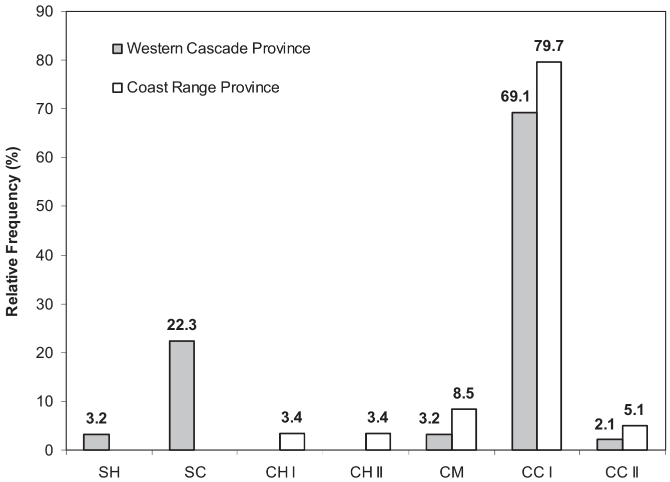
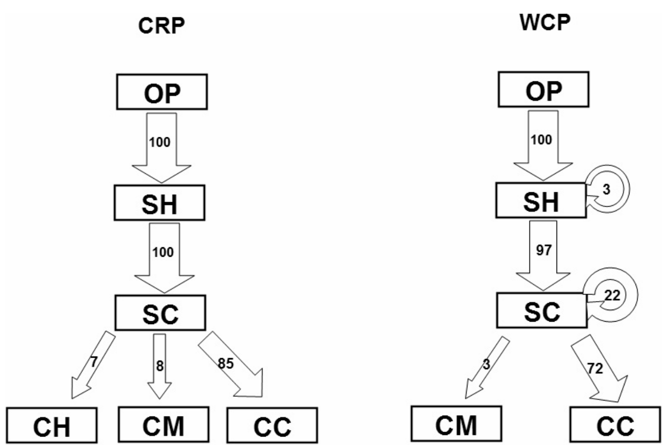


Fig. 7. Successional stage transition for the Coast Range Province (left) and the Western Cascades Province (right).



cades Province and Coast Range Province. Time to reach maximum absolute growth rate (Tmax Rate), time to reach 70% conifer cover (T70), and active growth period (AGP) showed similar patterns among sample stands, both across and within provinces (Fig. 8, Table 4).

Of the succession parameters examined, the correlation of DELAY with succession rate (i.e., wmAGR) is the lowest (r = –0.17) (Table 5). The parameters T70 and the 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 the most meaningful successional rate descriptors.

Discussion

Successional trajectories and rates

The direction, rate, and magnitude of vegetation change after stand-replacing disturbance are affected by disturbance intensity, environment, and stochastic features of many processes. Therefore, following disturbance, multiple successional pathways are commonly observed (Noble and Slatyer 1980; Abrams et al. 1985; McCune and Allen 1985) with rates of recovery highly variable (Halpern 1988; Myster and Pickett 1994).

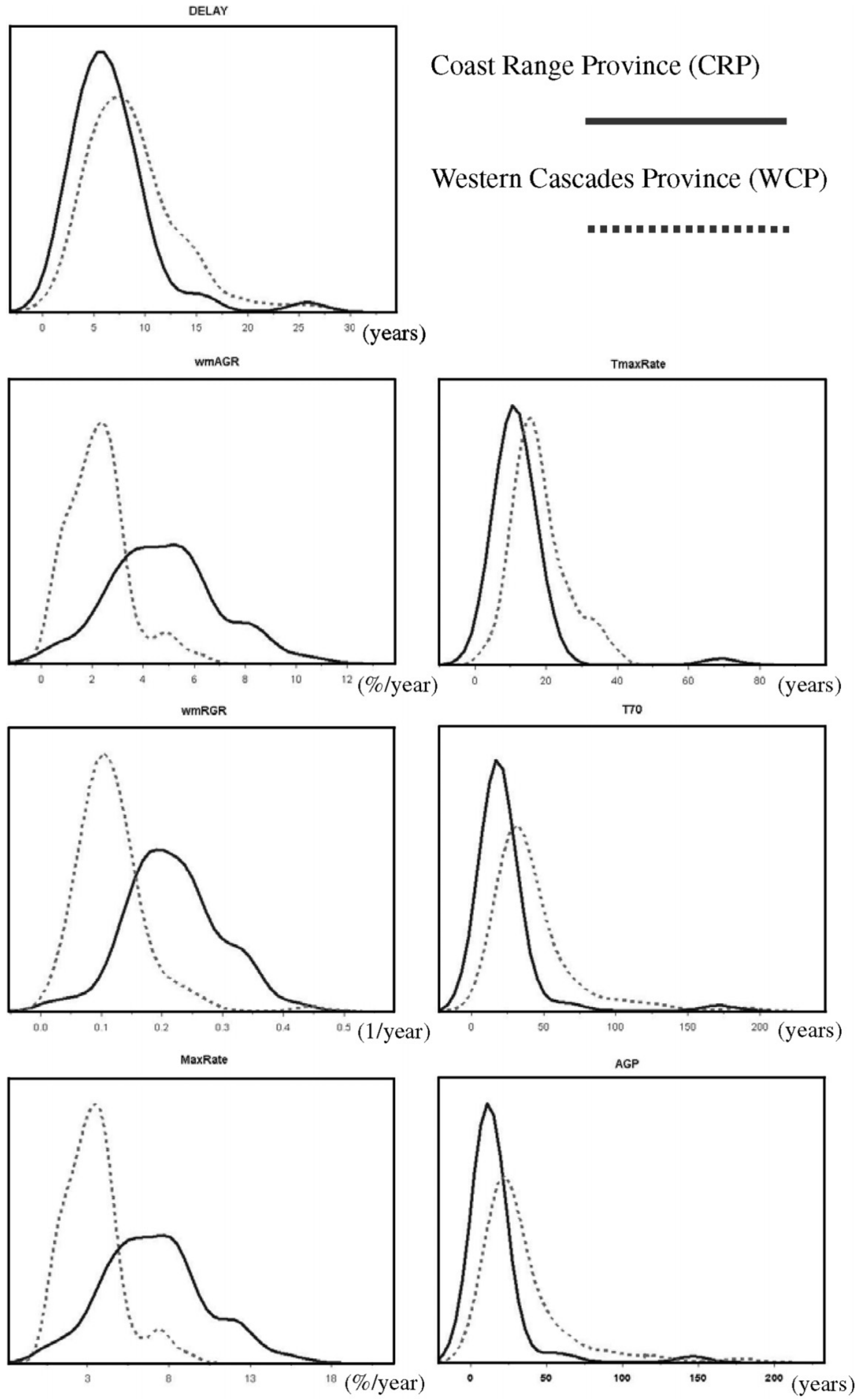
In this study, we defined succession as a process of changing life forms over time, and we used canopy cover data to define successional stages and represent trajectories. For simplicity, we described successional trajectories using the successional stage at age 50 (Table 2), modified by transition states at younger ages. We classified successional trajectories into seven different categories (Fig. 2).

The underlying common trends for both the Coast Range Province and Western Cascades Province 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 dominance by a conifer life form was not the same for all the stands, with a multiplicity of successional trajectories being manifested in both the sequence of change in successional stages and different transition times between successive stages because of different succession rates.

Both the photointerpreted data and modeled data showed that in the Coast Range Province a significant proportion of disturbed stands experienced a prolonged period of hardwood and mixed tree cover, whereas this was uncommon in the Western Cascades Province. This observation agrees with existing knowledge for these two provinces (Franklin and Dyrness 1988). The Coast Range Province contains both the Sitka spruce zone and western hemlock zone, whereas the Western Cascades Province 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). Hardwood trees can rapidly occupy disturbed stands (Zavitkovski and Stevens 1972), and the replacement of hardwood trees by conifer trees can be a slow process, because of the dense understory in hardwood stands (Meurisse and Youngberg 1971). Hardwood stands are not common in forests of the western hemlock zone even in the Coast Range Province, except on very recently disturbed sites or in riparian zones (Franklin and Dyrness 1988). However, hardwood life forms are known to occur in the riparian zone of both the Coast Range Province and Western Cascades Province. Based on the land cover for Oregon from Oregon Gap Analysis (1998), most of the samples belonging to the closed hardwood and closed mixed categories occurred within the Sitka spruce zone. In the Western Cascades Province, we also observed that about 3% of the sampled stands followed the SH trajectory and about 22% followed the SC trajectory, whereas no sample stands in Coast Range Province 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 1974*a*; Burrows 1990) or as rate of change in vegetation composition (Major 1974*b*; Prach 1993). As 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

Fig. 8. Distribution of successional rate parameters.



successional rate in our analyses. Because we were interested in early forest succession, the terminal stage for our purposes was when 70% conifer cover was reached. The derived parameter T70 from the Chapman–Richards function represents one interpretation of successional rate. However, instead of using similarity measures for species turnover, we used conifer life form and canopy cover change rates derived from the 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 life form and canopy cover data obtained from aerial photointerpretation,

Table 4. Comparison of successional rate characteristics.

	Western Cascades Province		Coast Range Province		
Parameter	Mean	SD	Mean	SD	*p* value of *t* test
DELAY (years)	8.80	4.45	6.60	3.98	<0.01
wmRGR (1/year)	0.12	0.06	0.22	0.08	<0.01
wmAGR (%/year)	2.26	1.19	4.82	2.11	<0.01
MaxRate (%/year)	3.36	1.74	7.12	3.09	<0.01
TmaxRate (years)	18.20	7.72	12.4	8.88	<0.01
T70 (years)	42.30	28.24	22.9	23.32	<0.01
AGP (years)	33.50	27.67	16.2	20.94	<0.01

Note: Parameter abbreviations are explained in Table 3. SD, standard deviation.

Table 5. Correlation matrix for successional rate characteristics.

Parameter	DELAY	wmRGR	wmAGR	MaxRate	TmaxRate	T70	AGP
DELAY	1						
wmRGR	–0.385	1					
wmAGR	–0.169	0.904	1				
MaxRate	–0.178	0.912	0.999	1			
TmaxRate	0.880	–0.624	–0.441	–0.450	1		
T70	0.391	–0.589	–0.640	0.592	–0.640	1	
AGP	0.247	–0.556	–0.646	0.478	–0.645	0.988	1

Note: Parameter abbreviations are explained in Table 3. Units for the parameters are the following: DELAY (years), wmRGR (1/year), wmAGR (%/year), MaxRate (%/year), TmaxRate (years), T70 (years), AGP (years).

which makes it possible to compare data sets for stands of different origin. However, the analysis was limited by the amount of information we could easily derive from photointerpretation. In this study, only dominance of canopy cover was examined with photointerpretation data, and no data about species and understory were used, which could otherwise provide important information on the likely future succession of a given stand.

As we defined it, succession was generally faster in the Coast Range Province than in the Western Cascades Province. The average time required to reach 70% conifer cover for Coast Range Province samples was 23 years, shorter than the 42 years required for the Western Cascades Province. Also, the rate measurements (wmAGR, wmRGR, maxRate) indicated that the average rate for the Coast Range Province was about double that of the Western Cascades Province (Fig. 8).

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 Coast Range Province than in the Western Cascades Province, and fog and low clouds in the Coast Range Province help to alleviate moisture stress for the drier summer period. Soil in the Coast Range Province is relative deep, rich, and fine textured compared with soil in the Western Cascades Province (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 patterns of environmental factors, such as precipitation and temperature.

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

We demonstrated that succession after stand-replacing disturbance was highly variable across western Oregon. In our study area, early succession differed in successional trajectory as influenced by the rate of succession. The quantification of successional trajectory, as was developed in this study, should be useful for modeling changes in regional carbon stores over time (Harmon et al. 1996). Variations in early forest succession could result in diverse forest structures that play many roles in ecosystems, for example, provide different habitats for many species (Spies 1998). Understanding of early forest successional trajectory can aid in forest management strategies for a wide range of forest goods and services (Spies et al. 1991; McComb et al. 1993).

Conclusions

In this study, we evaluated early forest succession by characterizing changes of life form (shrub and (or) herb, hardwood tree, conifer tree) and cover using air photos. We defined seven categories of successional trajectory and a set of parameters to describe the successional patterns. Our analysis indicated that conifer cover development in the Coast Range Province and Western Cascades Province differs in terms of succession rate and delay factors.

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 and contribution of top-down biogeoclimatic controls on successional trajectories, rate of succession, and transition delays is a next critical step. Such stratification by biogeoclimatic variables will enable us to partition geographic patterns of variance in various parameters of succession and thereby find collaborating influences of bottom-up topoedaphic controls.

Acknowledgements

This research was funded by NASA's Land User Land Cover Change and Terrestrial Ecology Programs. We greatly thank Willamette National Forest and Siuslaw National Forest of the USDA Forest Service for providing access to historical aerial photos for this research.

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