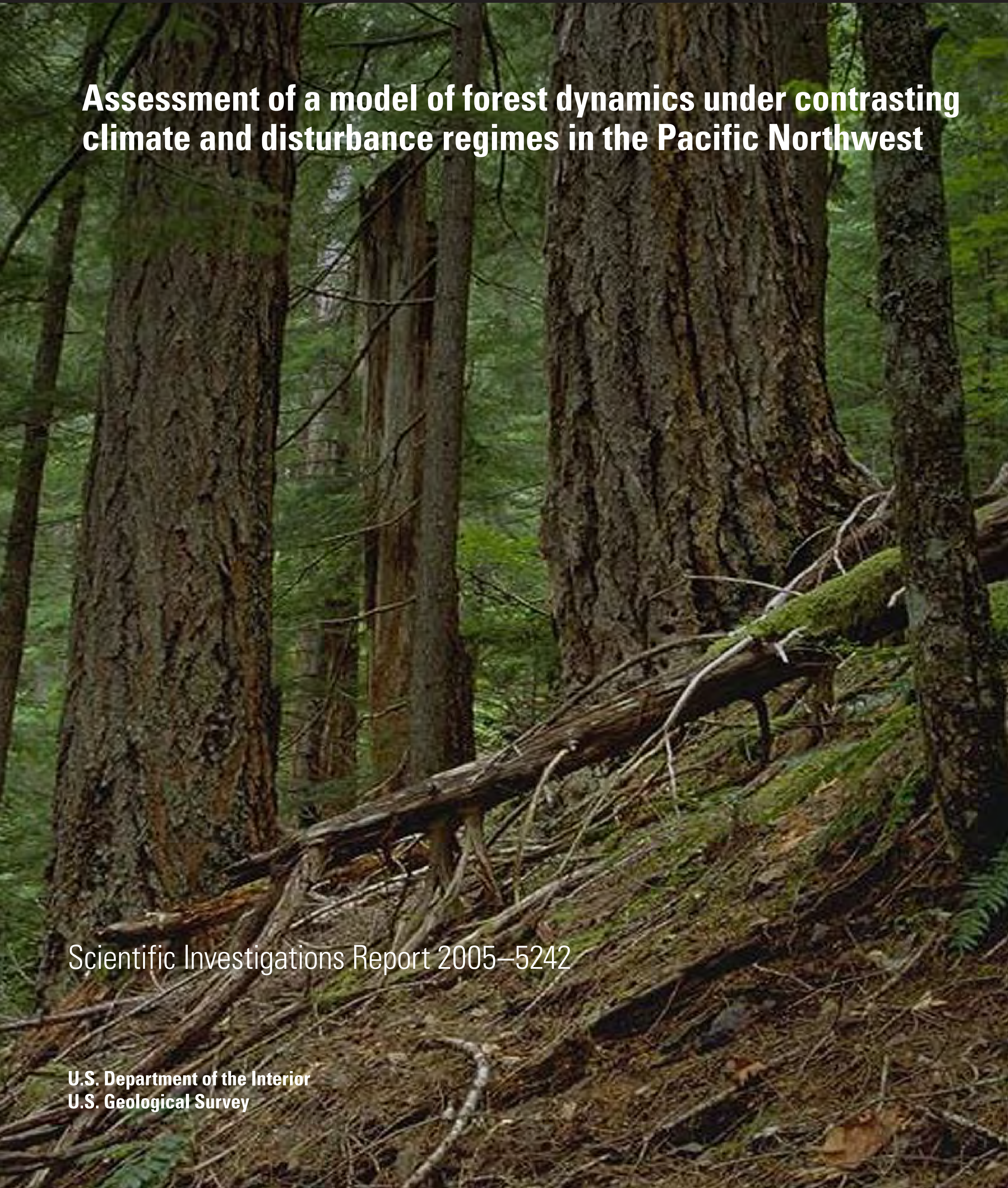
USGS
science for a changing world

Assessment of a model of forest dynamics under contrasting climate and disturbance regimes in the Pacific Northwest



Scientific Investigations Report 2005–5242

U.S. Department of the Interior
U.S. Geological Survey

Assessment of a model of forest dynamics under contrasting climate and disturbance regimes in the Pacific Northwest

By Richard T. Busing and Allen M. Solomon

Scientific Investigations Report 2005–5242

U.S. Department of the Interior
U.S. Geological Survey

U.S. Department of the Interior
Gale A. Norton, Secretary

U.S. Geological Survey
P. Patrick Leahy, Acting Director

U.S. Geological Survey, Reston, Virginia: 2005

For product and ordering information:
World Wide Web: http://www.usgs.gov/pubprod
Telephone: 1-888-ASK-USGS

For more information on the USGS--the Federal source for science about the Earth, its natural and living resources, natural hazards, and the environment:
World Wide Web: http://www.usgs.gov
Telephone: 1-888-ASK-USGS

Cover photo courtesy of USFS PNW-OSU Forest Science Data Bank

Contents

Figures

Tables

Conversion Factors

Multiply	By	To obtain
Area		
acre	4,047	square meter (m^2)
acre	0.4047	hectare (ha)
acre	0.4047	square hectometer (hm^2)
acre	0.004047	square kilometer (km^2)
square foot (ft^2)	929.0	square centimeter (cm^2)
square foot (ft^2)	0.09290	square meter (m^2)
basal area in square meters per hectare	4.36	square feet per acre
Density		
density in stems per hectare	0.405	stems per acre

DBH is the abbreviation for stem diameter at breast height (1.37 m above ground)

Horizontal coordinate information is referenced to North American Datum of 1983 (NAD 83). Vertical coordinate information is referenced to the North American Vertical Datum of 1988 (NAVD 88)

Altitude, as used in this report, refers to distance above the vertical datum.

Assessment of a model of forest dynamics under contrasting climate and disturbance regimes in the Pacific Northwest

Richard T. Busing and Allen M. Solomon

Abstract

An individual-based model of forest dynamics (FORCLIM) was tested for its ability to simulate forest composition and structure in the Pacific Northwest region of North America. Simulation results across gradients of climate and disturbance were compared to forest survey data from several vegetation zones in western Oregon. Modelled patterns of tree species composition, total basal area and stand height across climate gradients matched those in the forest survey data. However, the density of small stems (<50 cm DBH) was underestimated by the model. Thus actual size-class structure and other density-based parameters of stand structure were not simulated with high accuracy. The addition of partial-stand disturbances at moderate frequencies (<0.01 yr^{-1}) often improved agreement between simulated and actual results. Strengths and weaknesses of the FORCLIM model in simulating forest dynamics and structure in the Pacific Northwest are discussed.

Introduction

The individual-based model FORCLIM simulates forest dynamics in response to climate and natural disturbance (Bugmann, 1996). The FORCLIM "gap model" (sensu Shugart, 1984) is designed to capture the effects of climate regime on forest composition. In projecting forest composition it has performed well in several temperate forest regions (Bugmann & Solomon, 1995), including the Pacific Northwest (Bugmann & Solomon, 2000), where simulated patterns of forest vegetation along climate gradients have agreed well with generalized patterns of composition (e.g. Franklin & Dyrness, 1988). Exploration of how well the FORCLIM model reproduces characteristics of actual forest vegetation in the Pacific Northwest is only beginning (Busing & Solomon, 2004), however.

Background

Efforts to apply a single model of forest vegetation dynamics across broad environmental gradients have met with limited success. There are two general approaches to quantitative modeling of forest response to climate (Gates, 1993): 1) empirical models that relate biogeographic distributions of tree species to patterns of climate, and 2) mechanistic simulation models driven by the effects of climate on the performance of trees. A strength of mechanistic simulation models of forest dynamics is that they incorporate the biological and environmental processes underlying change. Thus far, ecological forest simulation models have been successfully parameterized and validated with empirical data at one or a handful of sites (Shugart, 1984; Botkin, 1992; Bugmann, 2001). Rarely have they been compared to extensive field data from biogeographic regions.

In the Pacific Northwest region of the United States and Canada several studies have considered forest response to climate using ecological models of forest gap (or patch) dynamics. Dale and Franklin (1989) projected minor compositional changes in *Pseudotsuga menziesii* forests subject to warming. Although *Pseudotsuga* and *Tsuga heterophylla* were projected to remain as forest dominants, *Abies amabilis*, a codominant species, was replaced by *Abies grandis*. Urban et al. (1993) modeled Oregon forest responses to climatic warming, but presented quantitative results on general ecosystem parameters rather than forest composition. Cumming and Burton (1996) examined the responses of eight forest vegetation zones in British Columbia to climatic change. Under climatic warming they noted potential changes in composition and productivity. They projected that *Pseudotsuga menziesii* would expand northward into forests currently dominated by *Picea* and *Pinus*. They also warned that coastal forests may suffer if winter-chilling requirements are not met. Zolbrod and Peterson (1999) modelled responses to climatic warming in the subalpine forests of the Olympic Mountains. Major shifts in coniferous species composition were projected for the present-day subalpine zone under various potential climate regimes.

Models used in the simulations above are based on several simplifying assumptions that have been questioned by several independent researchers (Bonan & Sirois, 1992; Pacala & Hurtt, 1993; Urban et al., 1993; Schenk, 1996; Loehle & LeBlanc, 1996; Bugmann & Cramer, 1998; Reynolds et al., 2001). The assumptions in question tend to revolve around the effects of climate on tree performance. In response to several of these criticisms, Bugmann and Solomon (2000) revised the simulation of climate effects on trees (see Methods). Using their revised model, they were able to generate reasonable forest composition and biomass across a broad climate gradient in western Oregon from wet and mild coastal rainforests to dry interior zones lacking trees. With a few exceptions, their projections of quasi-equilibrium forest composition matched general patterns of potential natural vegetation (Franklin

& Dyrness, 1988). Initial comparisons between simulated composition and extensive quantitative data on actual forest composition in the Pacific Northwest indicated good agreement for forest composition at the ecoregion level (Busing & Solomon 2004).

Purpose and Scope

The objective of the current study is is to further evaluate simulated and actual forests. Quantitative assessments of simulated and actual forest composition and structure are provided. This is accomplished by comparing simulated forest attributes to actual attributes from recent field data from unlogged forest stands in advanced stages of succession and development (with trees exceeding 150 years in age). Implications for forest stand and landscape dynamics are considered by examining results within and among ecoregions.

How well the model captures features of actual forest stands such as the composition of tree species and the numbers and sizes of tree stems is evaluated along gradients of climate and disturbance. The following questions are addressed: 1) how well does the simplest model, assuming long-term forest development without exogenous disturbance, perform along climatic gradients? 2) does the consideration of stand-replacing disturbance improve agreement between simulated and actual forest composition and structure? 3) does the addition of partial-stand disturbances, which, in contrast to those above, occur as smaller asynchronous patches, further improve agreement with actual forest composition and structure?

Acknowledgements

The authors thank Harald Bugmann and Rusty Dodson for helpful advice on use of the model. Anita Risch and Daniel Mailly provided constructive comments on the draft manuscript. Henry Lee and Don Phillips provided advice on statistical analyses. The field data used in comparisons were collected under ecological survey programs of the U.S. Department of Agriculture and the U.S. Department of the Interior.

Description of Study Area

The climate of western Oregon is maritme, characterized by weak seasonality of temperature and strong seasonality of precipitation (Franklin & Dyrness, 1988). Mild, wet winters and cool, dry summers are typical of coastal areas (Fig. 1a). The range of annual temperature variation tends to increase inland (Fig. 1b). Montane areas are subject to high winter snowfall, but annual precipitation tends to decrease inland, particularly in low areas (Fig. 1b).

Forests of the region are dominated by evergreen conifers. Deciduous species are not competitive given the cool and dry conditions that prevail when they are in leaf (Daubenmire, 1978). By contrast, evergreen species can photosynthesize well beyond summer under the mild temperatures of early spring and late autumn. Mesic coniferous forests of the region are characterized by very large, long-lived tree species that comprise forests with unusually high basal area and biomass. Further information on vegetation and environment of the region is provided by Franklin and Dyrness (1988) and Franklin and Halpern (2000).

Methods

The model

The FORCLIM model is specifically designed for the study of forest response to climate gradients or contrasting climate regimes. Detailed information on the initial version of the model is provided by Bugmann (1994, 1996). It is an individual-based simulator of forest dynamics that can operate across a range of spatial and temporal scales (Bugmann & Solomon, 1995). The model applied (FORCLIM version 2.9) is the result of an evolution from JABOWA (Botkin et al., 1972), FORET (Shugart & West, 1977), FORECE (Kienast, 1987), and FORCLIM version 1.0 (Bugmann, 1994, 1996; Bugmann & Solomon, 1995). In this investigation, it is applied to the study of forest stand composition and structure along gradients of climate and disturbance in western Oregon.

FORCLIM is a gap model (sensu Shugart, 1984) in which a set of independently simulated plots, each representing a gap-sized patch, is taken to represent a forest stand (Bugmann, 1996). The model assumes that compositional and structural dynamics are driven by tree species responses to the dynamic biotic and abiotic environmental forces modelled and assessed annually for each plot. A pool of 20 tree taxa (18 species and two subspecies) common to northwestern Oregon is used in the current study. Key species parameters affecting dynamics include a maximum diameter at breast height (DBH), a maximum age, a unique set of resource-growth-response functions, and a set of conditions for ingrowth. General carrying capacity (or biomass capacity) functions are not used in FORCLIM, but rather represent emergent properties of the simulations.

An advanced version of FORCLIM is used in this study. Unique features of FORCLIM 2.9, a version developed for the strongly seasonal climate of the Pacific Northwest (United States), center on the effects of climate on tree performance (Bugmann & Solomon, 2000). The widely used parabolic curve of potential tree growth versus total annual degree days (Botkin et al., 1972; Shugart, 1984; Botkin, 1992) is replaced with an asymptotic curve assuming reduced potential growth only at the colder edge(s) of a species' range. A drought index is applied to constrain tree growth in the warmest portion of a species' geographic range, but is based on the species' moisture stress tolerance. The drought index is associated with a new submodel of water balance using a bucket model scheme

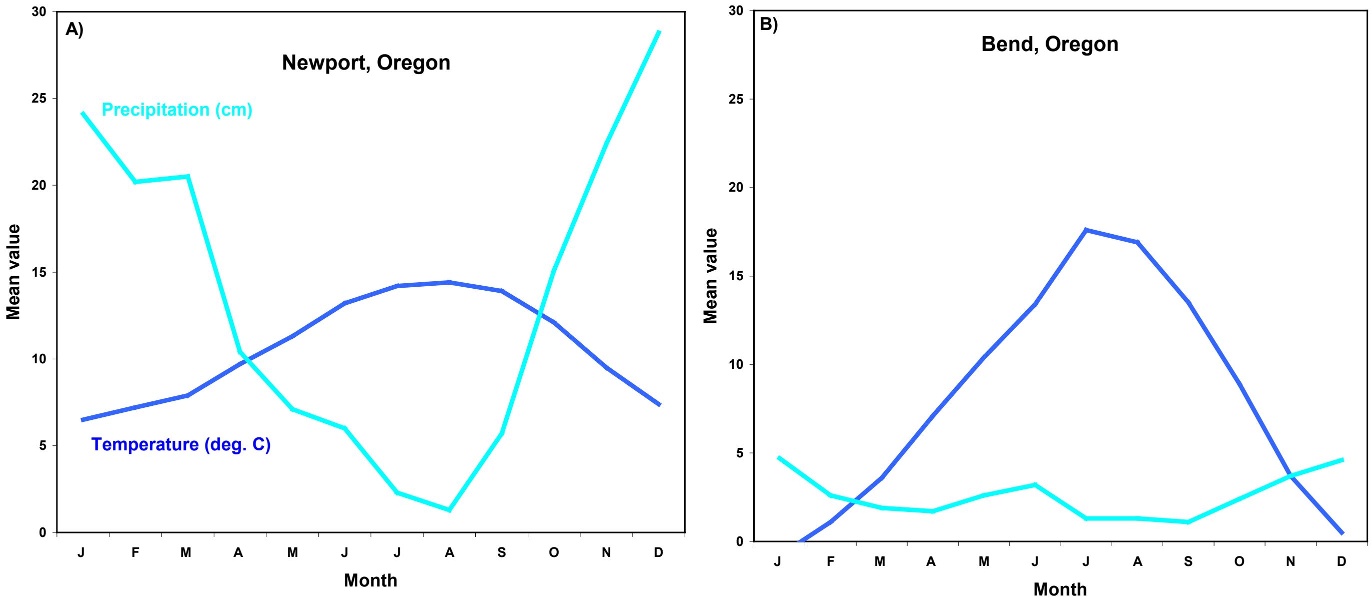


Figure 1. Graphs showing monthly temperature and precipitation data for two contrasting sites in western Oregon: a) coastal site (Newport), and b) inland site (Bend). All data are from Sternes (1960).

described in detail by Bugmann & Cramer (1998) rather than the more commonly used empirical model of Thornthwaite & Mather (1957). Monthly mean temperature and precipitation underlie climate calculations affecting annual growth of trees (e.g. Botkin et al., 1972; Shugart, 1984), but the potential growth of deciduous species is determined from climate data only for months when trees are in leaf (April to October). A winter chilling requirement is added to the regeneration "filters" (sensu Shugart, 1984) for each species. If the simulated minimum winter temperature for a year is too warm to permit winter dormancy as defined by a species-specific threshold value, then regeneration of the species is temporarily reduced. For further detail, see Bugmann & Solomon's (2000) discussion of these and other modifications leading to a version of FORCLIM suited to Pacific Northwest forests and climates.

Empirical data

A set of data on 2323 forest stands in western Oregon was assembled from USDA and USDI databases (Busing, 2004). All stands were inventoried after 1993 using USDA Forest Service conventions adopted for an ecological survey of forested federal lands (Max et al., 1996). In that system, known as the Current Vegetation Survey (CVS), plots were established on a square grid at 5.5 km intervals. A five-subplot design covering a 1-ha area was used for tree stratum observations at each plot site. Measurements on live trees included diameter at breast height and, for selected individuals at most sites, tree height and age. We selected sites in which all five subplots were inventoried and tree age data were collected.

Our analyses were restricted to all live trees >7.6 cm DBH. We calculated basal area for dominant species and for all species combined. Stand age, or time since the last stand-replacing disturbance, was estimated as the maximum age of a cored tree at each plot site. Climate data were assigned to each plot site using the geographic coordinates of the plot and the interpolated climate data sets described in Lugo et al. (2000).

Model comparisons with field data

Several tests of the ability of FORCLIM 2.9 to generate accurate vegetation patterns across environmental gradients were performed using the forest survey data set. These were performed among: 1) sites along a geographic transect across a series of vegetation types from wet, coastal forests to dry, continental steppe, and 2) sites within selected ecoregions representing much the variation in precipitation, temperature, and natural disturbance in western Oregon forests north of 43.5° N latitude. The critical input parameters varied among simulations were site monthly mean climate and, in certain cases, annual disturbance frequency. Species parameters followed Busing and Solomon (2004). They were held constant among simulations.

The first set of tests involved eight sites on a western Oregon transect along the 44.13° N parallel (Fig. 2; Bugmann & Solomon, 2000). Individual sites were chosen to represent a particular type of potential natural vegetation as described by Franklin and Dyrness (1988). Vegetation types (or zones) included coastal forests with *Pseudotsuga menziesii* and *Picea sitchensis*, mesic montane forests with *Pseudotsuga menziesii* and *Tsuga heterophylla*, subalpine forests with several species of *Abies* and *Tsuga mertensiana*, less mesic lowland forests with *Pseudotsuga menziesii* and *Abies grandis*, dry forest with *Pinus ponderosa*, and non-forest shrub-steppe. Simulations were run at each of the eight sites, which ranged from coastal to montane forests (7 sites) and interior steppe (1 site). Climate data, interpolated from existing long-term climate stations, were used for each site (Lugo et al., 2000). Simulated nutrient supplies were set at levels adequate to support tree growth, and natural disturbances other than canopy gap formation from endogenous tree mortality were not employed. In this case, endogenous mortality refers to the death of trees simulated as a probabilistic function of maximum lifespan (background mortality) or in association with limited tree growth (stress mortality). Simulated disturbance regimes did not differ among ecoregions. The primary abiotic environmental modifiers of tree growth were suboptimal temperatures and drought stress.

Field data representing each of the seven forested transect sites were selected from the pool of actual forest stands. Field plot sites known to have trees >150 yr in age were selected from a latitudinal belt between 43.63 and 44.63° N (except for the transect site at –123° W where a wider belt from 43.13 to 45.13° N was used to obtain adequate numbers of field plot sites). For each of the transect sites, field plots within 152 m elevation and 0.2° longitude of the transect site were used for comparison. Species basal area and total basal area were compared between simulated and actual data.

Initial simulations were run to 1500 yr, the longest maximum lifespan of any of the potential dominant tree species in the region. Simulations of this length served to project potential natural vegetation under various climate regimes at the transect sites. Durations of a second set of simulations matched the mean stand age of the actual plots representing forest vegetation near each transect site. All simulation runs consisted of 200 patches (or plots) of 0.0833 ha area, modelled independently. Simulation results were averaged across plots.

A second set of tests involved 6 forested ecoregions in western Oregon. Forested ecoregions (Omernik level IV classification; Thorson et al., 2002) centered north of 43.5° N latitude and having 20 or more field data sites with old trees (>150 yr) were used in the analysis (Fig. 3). For each ecoregion, measured basal area of dominant species, and total basal area of very shade-tolerant species (*Abies amabilis*, *Abies grandis*, *Picea sitchensis*, *Thuja plicata* & *Tsuga heterophylla*) characteristic of late succession served to quantify composition. Structure was assessed by ecoregion using total basal area of all species, quadratic mean tree diameter (diameter of trees with average basal area; Husch et al., 2003), tree density by diameter class, and weighted mean tree height (total cylindric wood volume divided by basal area; Whittaker, 1966). These same measures were calculated using simulated data from a randomly selected subset of field plot sites (n=20) within each ecoregion. Prior to the simulations, the selected field sites were tested to determine whether they represented the larger pool of eligible field sites available in the ecoregions. This was accomplished by examination of means and distributions for measured variables describing stand composition and structure. All analyses included only live trees >10 cm DBH.

Initial simulations were based on climate regime and age of the oldest tree (which dictated simulation length) at each randomly selected site. In additional simulations, regimes of exogenous disturbance were superimposed on the stands. Various regimes of partial disturbance in the form of severe small-scale events (0.08 ha), differing in disturbance frequency (range 0.0025 to 0.01 of land area yr^{-1}), were simulated by removing all trees on a patch. The year of disturbance was selected through independent probabilistic simulation among patches. The corresponding range of partial disturbance return intervals was 400 to 100 yr. The forest metrics noted above were compared within each ecoregion between various simulated stands and actual stands using top-down correlation (Iman & Conover, 1987) of species' basal area values for species composition, and t-tests for all other variables.

Results

Geographic transect

Seven of the eight transect sites were forested (Fig. 2). The easternmost site (-121° longitude) had non-forest vegetation. All simulations failed to grow trees at this site. For the seven forested sites the actual data agreed with mapped vegetation type classifications (Franklin & Dyrness, 1988). Tree species that were dominant or characteristic of actual late successional stands were dominant or present in each vegetation type classification (Fig. 4a). The same was true for the simulated data for 1500 yr stands (Fig. 4b). Furthermore, the decline in total basal area from west to east (inland) along the transect is captured in the simulations; however, total basal area and the basal area of various tree species in these long-term simulations often deviated sharply from the actual basal area. Total basal area projected by 1500-yr simulations was greater than actual basal area in most cases, and late successional species (e.g. *Abies amabilis*, *Abies grandis*, *Picea sitchensis*, *Thuja plicata*, and *Tsuga heterophylla*) were often over represented in these extended simulations. For species composition, agreement generally improved when simulation length was reduced to match mean age of the actual stands representing each site (range of mean values 245 to 426 yr) (Fig. 4c). In this case, simulated total basal areas exceeded the actual levels only in the four sites at the western (coastal) end of the transect (-121.96 to -124.1° longitude).

For all forest types considered, the mean total basal area across transect sites was 50 m^2ha^{-1} for the actual data. The corresponding value was 55 m^2ha^{-1} for the 1500-yr simulations, and 55 m^2ha^{-1} for the simulations adjusted to stand age. A parallel comparison of the mean relative basal area of very tolerant tree species, that are generally abundant only in late successional stands (see above), revealed lower proportions

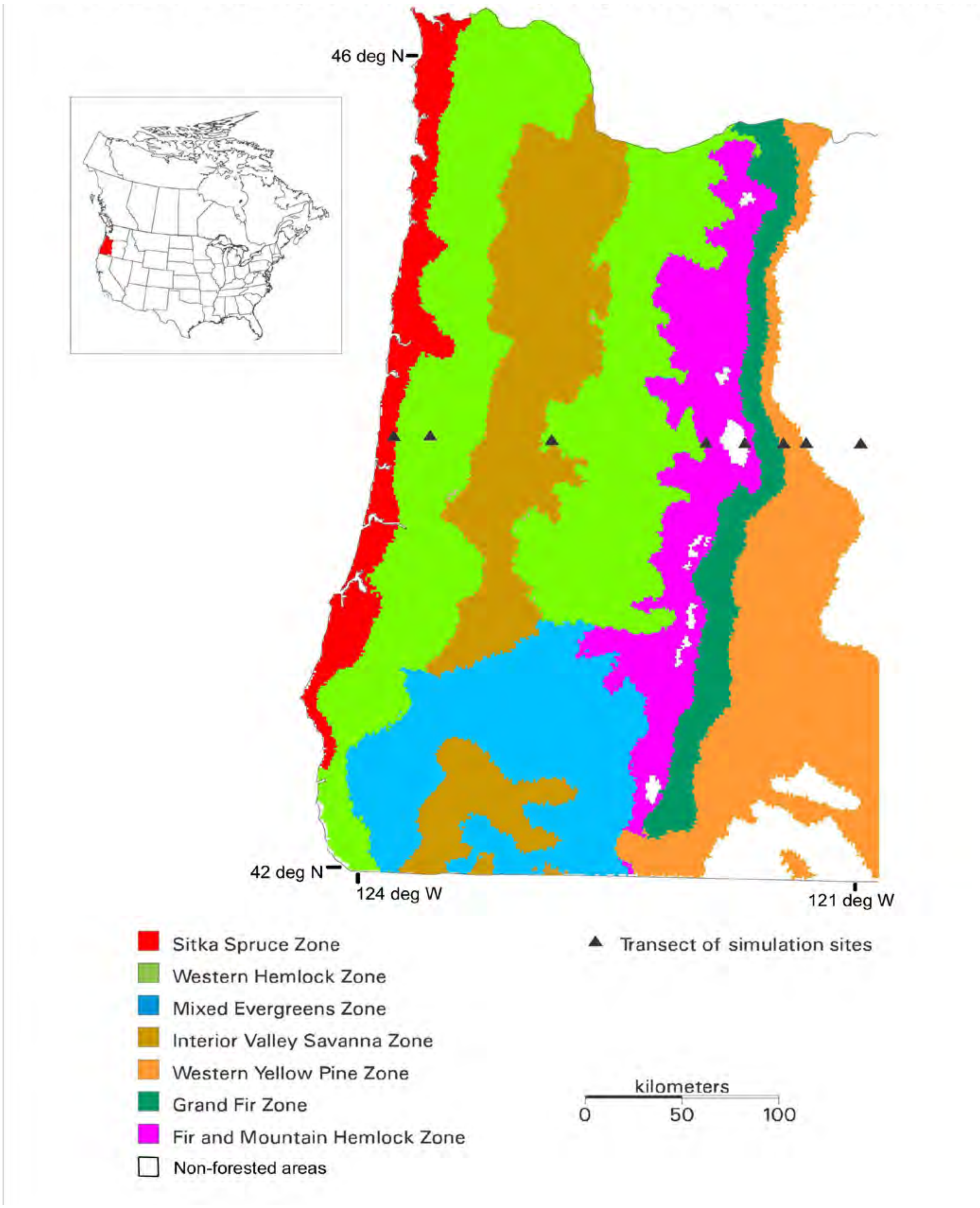


Figure 2. Map of western Oregon showing the location of sites along a transect at 44.13° N latitude.

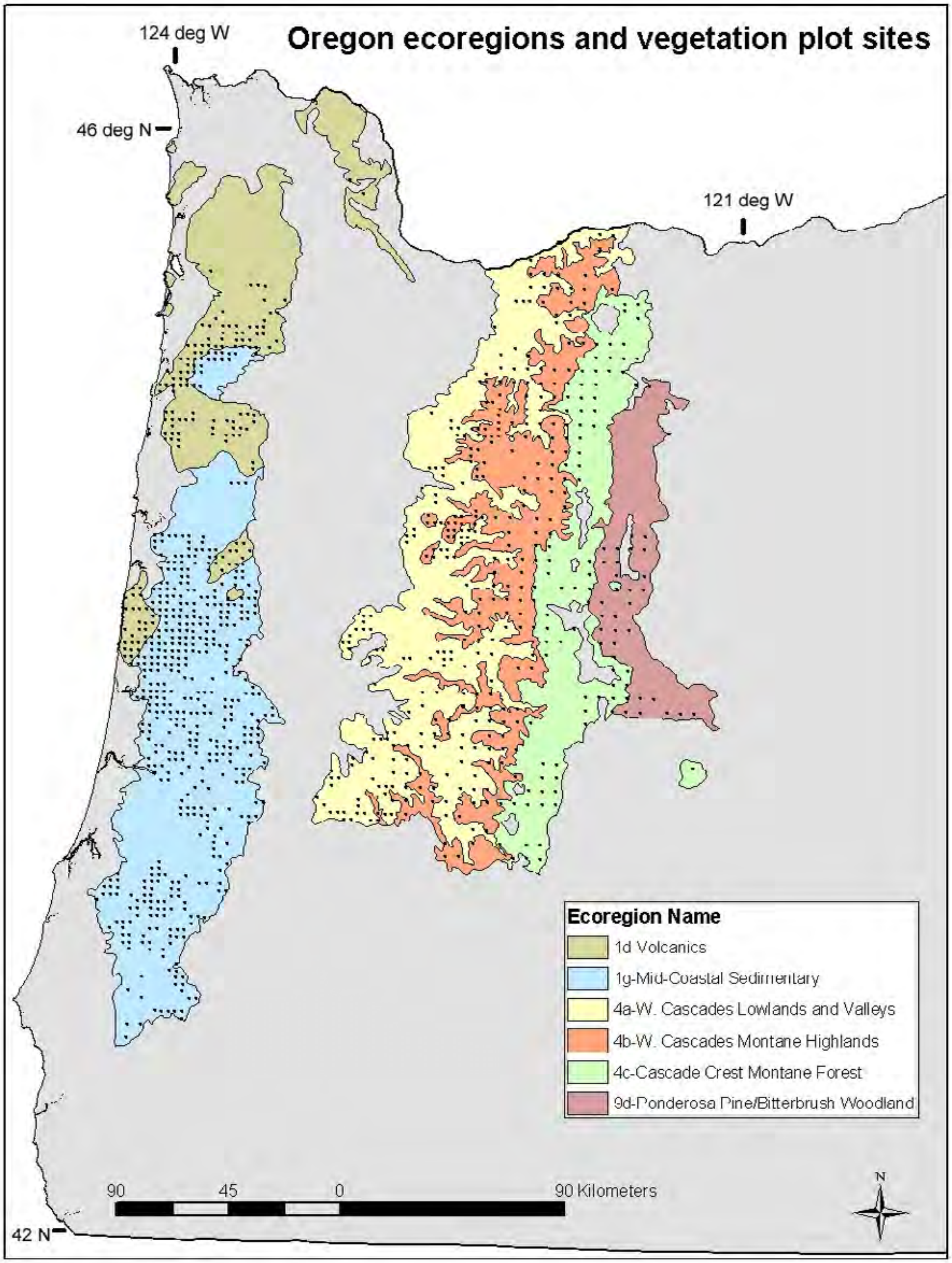


Figure 3. Map of western Oregon showing the ecoregions used for evaluation of the model. The pool of field plot sites located within each ecoregion are shown.

in actual stands. The actual proportion of very shade-tolerant species combined was 15%. In the 1500 yr simulations the corresponding value was 38%. In the simulations adjusted for stand age, the corresponding value was 23%.

Forested ecoregions

Composition by ecoregion

Within each of the seven forested ecoregions, all of the simulations generated tree species composition that was significantly ($P<0.05$) correlated with actual composition (Fig. 5; Table 1). Although the simulations spanned a broad range of partial disturbance regimes (frequency 0 to 0.01yr^{-1}), deviations from actual composition were few. All correlations were highly significant ($P<0.01$) in the Mid-Coastal Sedimentary and the Western Cascades Montane Highlands ecoregions. Three out of four simulations gave highly significant correlations in the Coastal Volcanics and the Cascade Crest ecoregions. Half of the simulations in the Ponderosa Pine ecoregion gave highly significant correlations. Only one out of four simulations in the Western Cascades Lowlands gave a highly significant correlation for composition.

The combined basal area of selected late successional species (see above) showed a response to simulated partial disturbance frequency (Table 2). In each ecoregion, imposing partial disturbance on the stands decreased the basal area of late successional species. Partial disturbance improved agreement between the simulated and actual proportions of late successional species. Except for the Ponderosa Pine ecoregion (9d) where late successional species were absent from the actual data, there were several regimes of partial disturbance that gave a simulated percentage of late successional species not significantly different from that of the actual data in a given ecoregion ($P>0.05$).

Among ecoregions, the combined basal area of simulated late successional species attained maximum levels in the western Cascade Range (Table 2). These levels declined near the coast and from the high Cascades eastward. The pattern was evident in both the simulated and actual data.

Structure by ecoregion

The fraction of simulated forest patches in disturbed condition (basal area < 20% of undisturbed average for ecoregion) varied strongly among partial disturbance regimes. Without partial disturbance the simulations gave a low fraction (<1% to 6% of total land area) of disturbed patches in all forested ecoregions (Table 3). This fraction increased with a higher frequency of partial disturbance and was particularly high under the maximum frequency simulated (0.01 yr^{-1} regime; 19-45% of total land area).

Across all ecoregions, total basal area generally declined inland (eastward). This trend was also noted in the geographic transect analysis. It held true for the simulated data as well as the actual data (Table 2). In the absence of partial disturbance, simulated total basal area exceeded the actual value for each of the seven forested ecoregions. In each ecoregion, a pattern of decreasing total basal area with increasing frequency of partial disturbance was evident. The addition of partial disturbance improved agreement between simulated and actual basal area.

Simulated total density of trees was often lower than actual density in a given ecoregion (Table 2). Even though simulated total density increased with increasing frequency of partial disturbance, in any given ecoregion, most, if not all, of the simulated densities were significantly lower ($P<0.05$) than actual density. However, agreement between simulated and actual densities improved when only large trees (>50 cm DBH) were considered (Table 2). Size-class structure in an ecoregion (e.g. ecoregion 4b) differed among actual and simulated data, and among simulated disturbance regimes (Fig. 6). Even though densities of small stems tended to increase with frequency of partial disturbance, the increases were not great enough to match actual densities.

Both the simulated and actual quadratic mean diameter and weighted mean height of trees were lowest in the easternmost (inland) ecoregions (Table 2). Within each ecoregion the simulations without partial disturbance gave values for these variables that exceeded actual values. Simulations with partial disturbance gave lower values, some of which matched actual values.

Discussion

Simulated patterns of forest change along broad climate gradients match patterns of potential natural vegetation in western Oregon. However, the long-term simulations (1500 yr) without exogenous disturbance, meant to project potential natural vegetation, generate forest stand characteristics that do not entirely match actual forest stand characteristics. For example, the simulated abundance of shade-tolerant species often exceeds the actual abundance of such species. Furthermore, the simulated amount of forest area in disturbed condition is atypically low. Even though the actual data are comprised only of old stands having trees >150 yr in age, the long-term simulations do not fully agree with actual forest composition and structure.

The consideration of exogenous, stand-replacing disturbance alters simulation results. When time since the last stand-replacing disturbance is included in the simulations, the basal area of shade-tolerant species tends to decrease and the fraction of land area in disturbed condition increases. The basal area of shade-tolerant species and the fraction of land area in disturbed condition are closer to actual levels. The improved agreement is expected because stand-replacing disturbances are an important component of the natural disturbance regime in this region (Franklin & Halpern, 2000). Nonetheless, simulated total basal area with stand-replacing disturbance, but without partial disturbance, tends to exceed

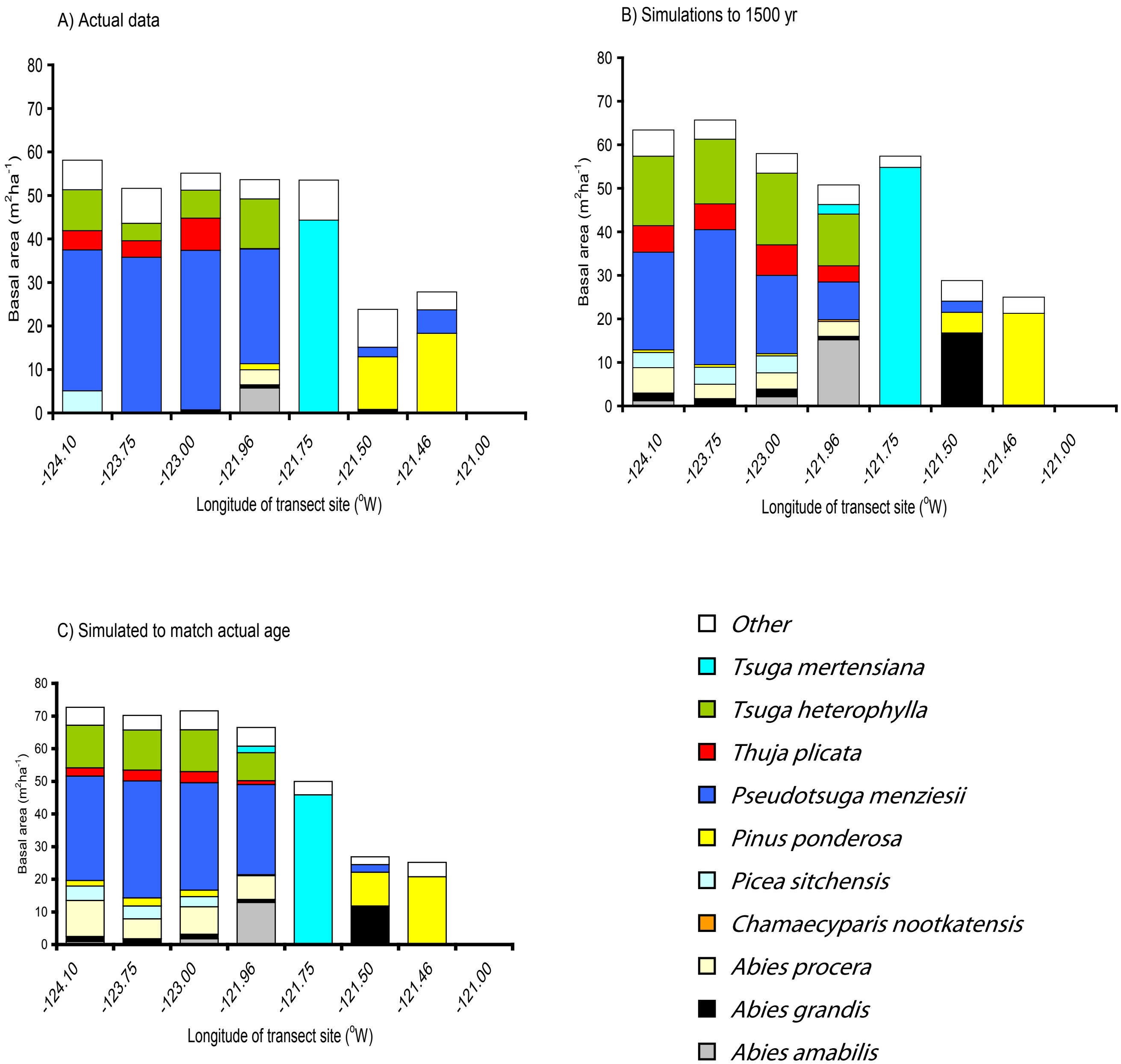


Figure 4. Graphs showing tree species composition and total basal area along the western Oregon transect at 44.13° N. Findings are presented for each transect site and data source. The sources of data are: a) actual field measurements; b) simulations at 1500 yr of forest development; and c) simulations with duration matching mean stand age of actual data near site.

Table 1. Top-down correlation results between actual and simulated tree species composition by ecoregion. All simulations account for stand-replacing disturbances; several also have partial disturbances as noted.

Simulated Data	Correlation Coefficient	z	P
Ecoregion 1d (Coastal Volcanics)			
No partial disturbance	0.815	2.446	0.007
Partial disturbance (freq. 0.0025 yr^{-1})	0.782	2.346	0.009
Partial disturbance (freq. 0.005 yr^{-1})	0.635	1.906	0.028
Partial disturbance (freq. 0.01 yr^{-1})	0.782	2.346	0.009
Ecoregion 1g (Mid-Coastal Sedimentary)			
No partial disturbance	0.97	2.91	0.002
Partial disturbance (freq. 0.0025 yr^{-1})	0.953	2.86	0.002
Partial disturbance (freq. 0.005 yr^{-1})	0.927	2.78	0.003
Partial disturbance (freq. 0.01 yr^{-1})	0.927	2.78	0.003
Ecoregion 4a (West Cascades Lowlands)			
No partial disturbance	0.871	2.613	0.004
Partial disturbance (freq. 0.0025 yr^{-1})	0.76	2.279	0.011
Partial disturbance (freq. 0.005 yr^{-1})	0.743	2.23	0.013
Partial disturbance (freq. 0.01 yr^{-1})	0.743	2.23	0.013
Ecoregion 4b (West Cascades Montane)			
No partial disturbance	0.895	2.686	0.004
Partial disturbance (freq. 0.0025 yr^{-1})	0.908	2.724	0.003
Partial disturbance (freq. 0.005 yr^{-1})	0.936	2.809	0.002
Partial disturbance (freq. 0.01 yr^{-1})	0.903	2.712	0.003
Ecoregion 4c (Cascade Crest Montane)			
No partial disturbance	0.832	2.496	0.006
Partial disturbance (freq. 0.0025 yr^{-1})	0.836	2.507	0.006
Partial disturbance (freq. 0.005 yr^{-1})	0.8	2.401	0.008
Partial disturbance (freq. 0.01 yr^{-1})	0.759	2.278	0.011
Ecoregion 9d (Ponderosa Pine Woodland)			
No partial disturbance	0.688	2.064	0.02
Partial disturbance (freq. 0.0025 yr^{-1})	0.829	2.488	0.006
Partial disturbance (freq. 0.005 yr^{-1})	0.688	2.064	0.02
Partial disturbance (freq. 0.01 yr^{-1})	0.829	2.488	0.006

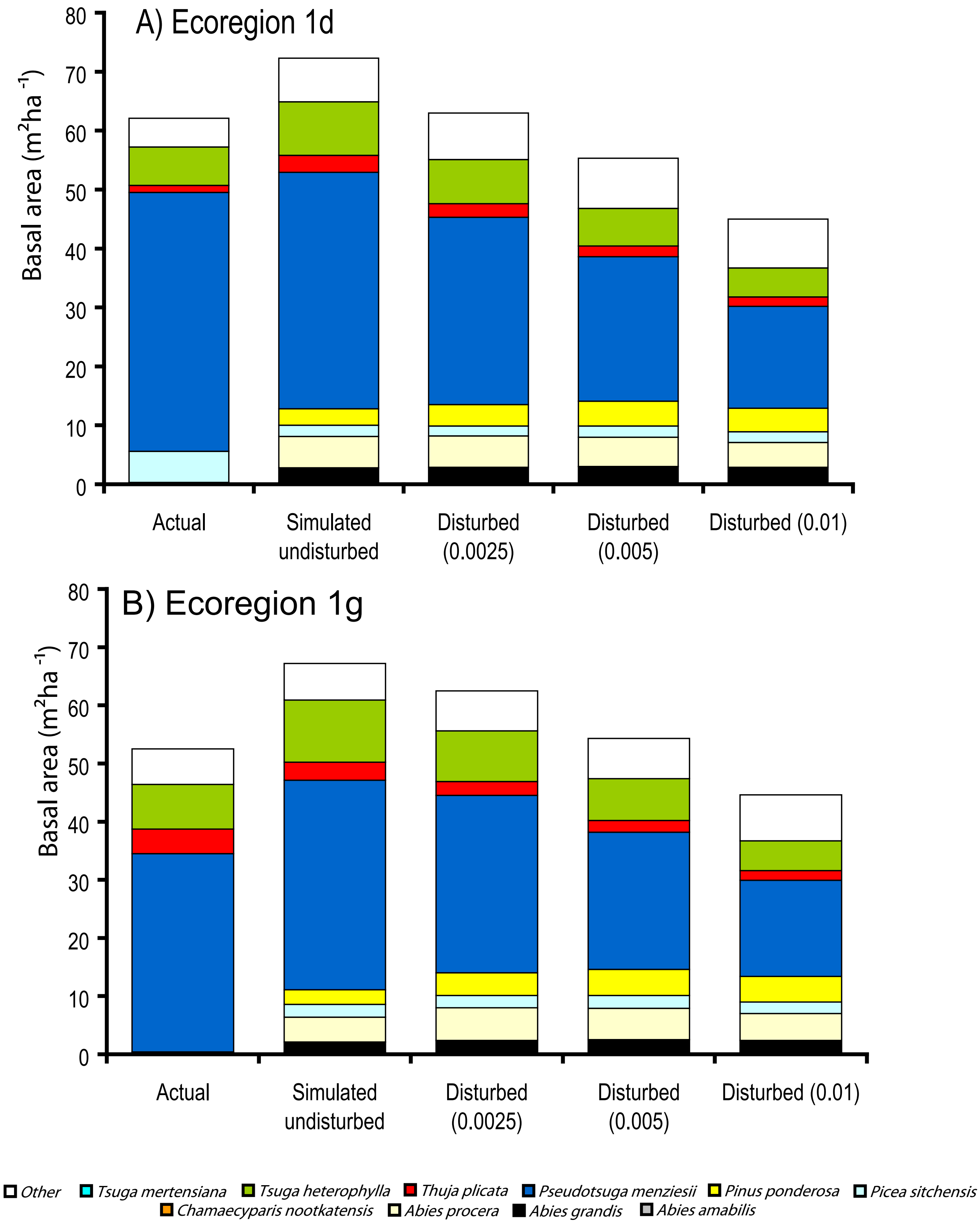


Figure 5. Graphs showing tree species composition and total basal area by ecoregion. Findings are presented by ecoregion: a) Coastal Volcanics (code 1d); b) Mid-Coastal Sedimentary (code 1g); c) W. Cascades Lowlands and Valleys (code 4a); d) W. Cascades Montane Highlands (code 4b); e) Cascade Crest Montane Forest (code 4c); and f) Ponderosa Pine (code 9d). Within each ecoregion, summaries for the various data sources are presented in the following order from left to right: 1) actual field measurements; 2) simulations with duration matching stand ages of the field sites selected within each ecoregion; 3) simulations with partial disturbance added (frequency 0.0025 yr^{-1}); 4) simulations with partial disturbance added (frequency 0.005 yr^{-1}); and 5) simulations with partial disturbance added (frequency 0.01 yr^{-1}).

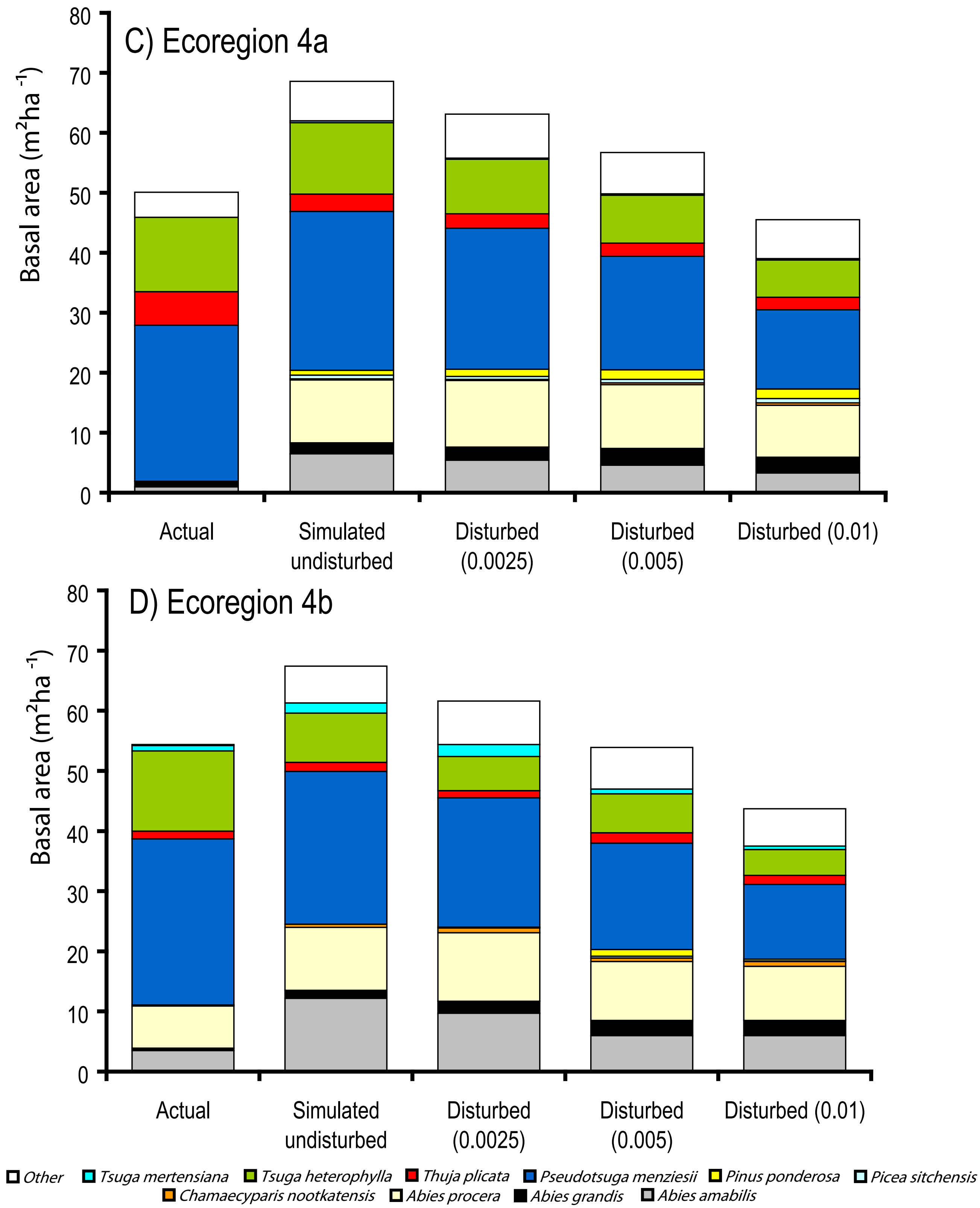


Figure 5—continued. Graphs showing tree species composition and total basal area by ecoregion. Findings are presented by ecoregion: a) Coastal Volcanics (code 1d); b) Mid-Coastal Sedimentary (code 1g); c) W. Cascades Lowlands and Valleys (code 4a); d) W. Cascades Montane Highlands (code 4b); e) Cascade Crest Montane Forest (code 4c); and f) Ponderosa Pine (code 9d). Within each ecoregion, summaries for the various data sources are presented in the following order from left to right: 1) actual field measurements; 2) simulations with duration matching stand ages of the field sites selected within each ecoregion; 3) simulations with partial disturbance added (frequency 0.0025 yr^{-1}); 4) simulations with partial disturbance added (frequency 0.005 yr^{-1}); and 5) simulations with partial disturbance added (frequency 0.01 yr^{-1}).

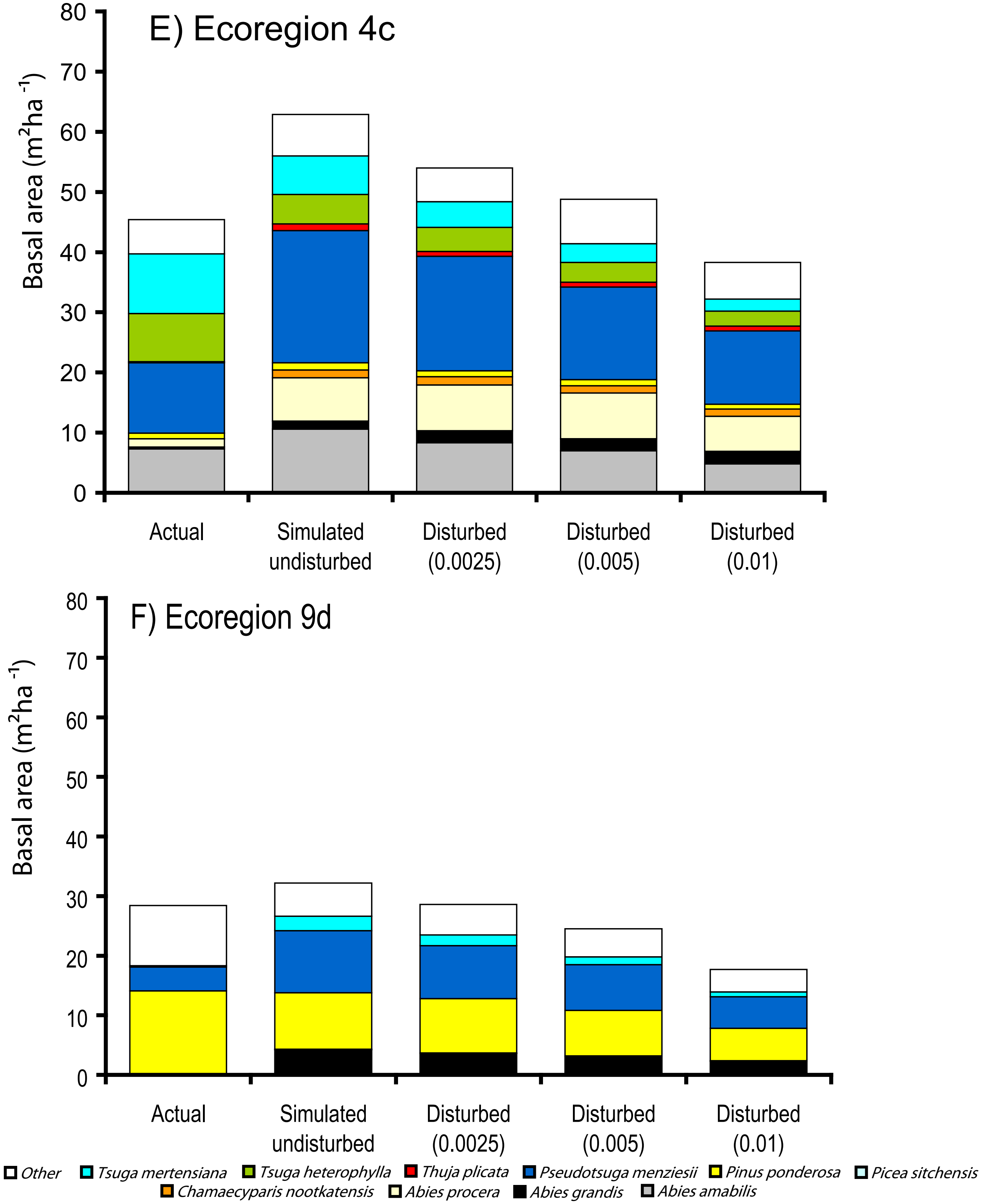


Figure 5—continued. Graphs showing tree species composition and total basal area by ecoregion. Findings are presented by ecoregion: a) Coastal Volcanics (code 1d); b) Mid-Coastal Sedimentary (code 1g); c) W. Cascades Lowlands and Valleys (code 4a); d) W. Cascades Montane Highlands (code 4b); e) Cascade Crest Montane Forest (code 4c); and f) Ponderosa Pine (code 9d). Within each ecoregion, summaries for the various data sources are presented in the following order from left to right: 1) actual field measurements; 2) simulations with duration matching stand ages of the field sites selected within each ecoregion; 3) simulations with partial disturbance added (frequency 0.0025 yr^{-1}); 4) simulations with partial disturbance added (frequency 0.005 yr^{-1}); and 5) simulations with partial disturbance added (frequency 0.01 yr^{-1}).

Table 2. Results of t-tests between actual and simulated variables of tree species composition and structure by ecoregion. Means, standard deviations and statistical significance levels (P) are provided. All simulations account for stand-replacing disturbances; several also have partial disturbances as noted.

Data source	Total basal area (square m/ha)			Late successional species basal area (square m/ha)			Total density (stems/ha)			Large tree density (stems >50 cm DBH/ha)			Quadratic mean diameter (cm DBH)			Weighted mean height (m)		
	Mean	S.D.	P	Mean	S.D.	P	Mean	S.D.	P	Mean	S.D.	P	Mean	S.D.	P	Mean	S.D.	P
Ecoregion 1d (Coastal Volcanics)																		
Actual	61	20		13	22		370	348		77	32		58	25		42	210	
Simulated, no partial disturbance	72	4	0.027	17	6	0.469	133	20	0.007	49	4	<0.001	84	6	<0.001	56	2	<0.001
Partial disturbance (freq. 0.0025/yr)	63	3	0.718	14	5	0.767	164	19	0.016	55	4	0.005	70	4	0.039	52	1	<0.001
Partial disturbance (freq. 0.005/yr)	55	2	0.196	13	5	0.955	192	23	0.034	57	5	0.011	61	4	0.575	48	1	0.02
Partial disturbance (freq. 0.01/yr)	45	2	0.001	11	4	0.736	228	23	0.083	54	5	0.004	50	3	0.226	43	2	0.833
Ecoregion 1g (Mid-Coastal Sedimentary)																		
Actual	52	24		12	10		286	166		68	47		56	19		43	6	
Simulated, no partial disturbance	71	5	0.002	19	6	0.016	129	10	<0.001	47	5	0.056	84	5	<0.001	56	1	<0.001
Partial disturbance (freq. 0.0025/yr)	63	3	0.059	13	5	0.176	159	18	0.003	53	3	0.174	71	4	0.002	52	1	<0.001
Partial disturbance (freq. 0.005/yr)	55	2	0.639	14	4	0.451	185	15	0.01	55	3	0.225	62	3	0.206	48	1	<0.001
Partial disturbance (freq. 0.01/yr)	45	3	0.18	11	3	0.738	231	20	0.157	54	4	0.181	50	2	0.166	42	1	0.885
Ecoregion 4a (West Cascades Lowlands)																		
Actual	49	24		19	15		517	307		60	45		39	16		35	9	
Simulated, no partial disturbance	69	5	0.002	24	3	0.176	139	18	<0.001	49	6	0.302	80	4	<0.001	55	2	<0.001
Partial disturbance (freq. 0.0025/yr)	63	4	0.014	20	2	0.827	175	17	<0.001	57	4	0.793	68	4	<0.001	51	1	<0.001
Partial disturbance (freq. 0.005/yr)	57	2	0.153	19	1	0.845	197	17	<0.001	61	4	0.909	61	3	<0.001	48	1	<0.001
Partial disturbance (freq. 0.01/yr)	45	3	0.526	15	1	0.244	239	20	0.001	55	5	0.628	49	3	0.009	42	1	0.001
Partial disturbance (freq. 0.01/yr)	18	7	0.004	2	3	0.001	153	65	<0.001	25	9	0.737	39	4	<0.001	31	4	<0.001

Table 2—Continued. Results of t-tests between actual and simulated variables of tree species composition and structure by ecoregion. Means, standard deviations and statistical significance levels (P) are provided. All simulations account for stand-replacing disturbances; several also have partial disturbances as noted.

Data source	Total basal area (square m/ha)			Late successional species basal area (square m/ha)			Total density (stems/ha)			Large tree density (stems >50 cm DBH/ha)			Quadratic mean diameter (cm DBH)			Weighted mean height (m)		
	Mean	S.D.	P	Mean	S.D.	P	Mean	S.D.	P	Mean	S.D.	P	Mean	S.D.	P	Mean	S.D.	P
Ecoregion 4b (West Cascades Montane)																		
Actual	53	24		19	16		398	280		82	49		49	25		37	8	
Simulated, no partial disturbance	67	6	0.019	25	3	0.105	156	15	0.001	52	5	0.011	74	5	<0.001	54	2	<0.001
Partial disturbance (freq. 0.0025/yr)	62	4	0.123	21	2	0.526	194	20	0.004	61	5	0.061	64	5	0.013	50	2	<0.001
Partial disturbance (freq. 0.005/yr)	56	6	0.678	18	2	0.815	219	24	0.01	61	4	0.066	57	6	0.161	47	3	<0.001
Partial disturbance (freq. 0.01/yr)	43	2	0.083	15	1	0.28	256	22	0.035	56	3	0.025	47	3	0.691	41	2	0.06
Ecoregion 4c (Cascade Crest Montane)																		
Actual	43	17		15	15		624	370		47	30		34	14		30	9	
Simulated, no partial disturbance	63	16	0.001	18	9	0.445	173	42	<0.001	56	15	0.244	69	10	<0.001	50	6	0.08
Partial disturbance (freq. 0.0025/yr)	56	14	0.015	15	7	0.955	208	46	<0.001	60	11	<0.001	59	8	<0.001	46	6	<0.001
Partial disturbance (freq. 0.005/yr)	49	11	0.244	13	6	0.634	227	44	<0.001	58	9	<0.001	52	7	0.147	43	5	0.028
Partial disturbance (freq. 0.01/yr)	38	10	0.292	10	5	0.189	252	44	<0.001	50	12	0.752	44	5	0.009	38	5	0.001
Ecoregion 9d (Ponderosa Pine Woodland)																		
Actual	26	10		0	0		527	223		24	21		26	6		22	6	
Simulated, no partial disturbance	34	14	0.054	4	5	0.002	121	72	<0.001	45	23	0.004	64	15	<0.001	40	6	<0.001
Partial disturbance (freq. 0.0025/yr)	29	12	0.408	4	4	0.001	141	69	<0.001	41	17	0.006	53	8	<0.001	37	5	<0.001
Partial disturbance (freq. 0.005/yr)	25	10	0.663	3	4	0.001	151	69	<0.001	36	13	0.034	47	6	<0.001	35	5	<0.001

Table 3. Amount of land in disturbed state by simulated partial disturbance regime and ecoregion. All simulations account for stand-replacing disturbances; several also have partial disturbances as noted. The percentage of total land area in disturbed condition at the end of each simulation period is provided. See Fig. 3 for ecoregion names.

Disturbance regime	Ecoregion					
	1d	1g	4a	4b	4c	9d
No partial disturbance	1	<1	<1	<1	1	6
Partial disturbance (freq. 0.0025 yr^{-1})	6	5	6	6	8	17
Partial disturbance (freq. 0.005 yr^{-1})	11	11	10	14	15	28
Partial disturbance (freq. 0.01 yr^{-1})	20	19	20	23	28	45

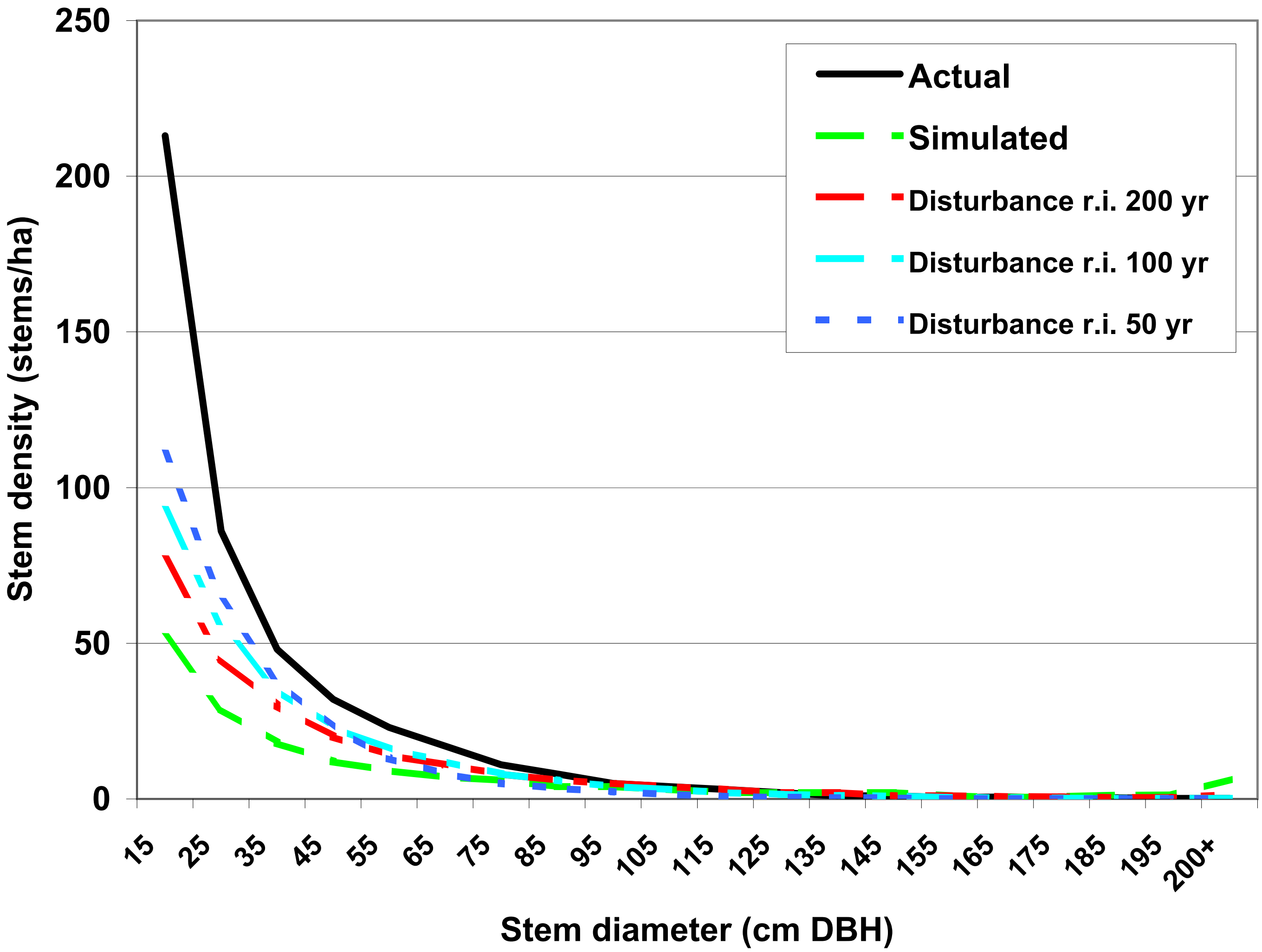


Figure 6. Graphs showing size-class structure of simulated and actual forest stands in ecoregion 4b. Actual stand data are indicated by a solid line. Dashed lines indicate simulated stand data under various return intervals of partial disturbance.

actual total basal area. This is particularly true in mesic forests west of the Cascade Range crest.

The basal area values from simulations corrected for stand-replacing disturbances still exceed mean actual values, but natural stands with considerably higher basal areas exist in the region. For example, stands selected for ecological study (e.g. Fujimori et al., 1976; Gholz, 1982; Acker et al. 1998) often have basal area values well above the mean values reported here for actual and simulated stands. Clearly, stands with such high basal area are either relatively undisturbed, relatively productive, or both. The fact that basal area levels from simulations accounting for stand-replacing disturbance tend to lie between the basal area values for selected, "optimum" study stands and mean values from extensive survey data is noteworthy. It suggests that consideration of stand-replacing disturbance is important, but other site factors such as productivity and exposure to partial-stand disturbances also influence basal area and structure.

Evidence that Pacific coniferous forests are influenced by partial-stand disturbance as well as catastrophic stand disturbance is accumulating (Franklin & Hemstrom, 1981; Harcombe, 1986; Agee, 1993). When partial-stand disturbances are added to the simulations, several structural variables show improved agreement with actual values. For example, total basal area and mean tree height more closely resemble their respective actual values. Effects on composition are also evident. Under partial disturbance, the basal area of late successional species tends to diminish to levels nearer to those of actual forests. The basal area of *Pseudotsuga* is noticeably affected by partial-stand disturbance frequency; however, correlations between simulated and actual composition remain strong.

A noticeable difference between simulated and actual composition was the presence of several species in the simulations that were rare or absent in the actual data. These species tended to be minor components of the simulated stands. Their presence reflected the fact that the factors limiting establishment and growth of tree species in the simulations are simplifications of reality. The most critical assumption in this regard was that species' propagules were available in all simulated stands. In reality they were probably available only in the vicinity of their rare parent trees, and hence, not consistently available at many sites. Assumptions of climatic tolerances also may have played a role. No simulated dominant species within the ecoregions examined were unanticipated given the climatic conditions simulated. Some discrepancies were noted for minor species, however. For example, *Picea sitchensis* was evident as a very minor species in some simulated montane forests. In reality it was rare except along the coast where fogs and warm winters enhance its growth.

Structural projections of the model reveal some deviations between simulated and actual forests. Although general geographic patterns in stand basal area and height are captured by the model, size-class structure is not fully captured. Both simulated and actual stands show a decline in number of stems with diameter class, but the number of small stems (<50 cm DBH) tends to be low in simulated stands. Total stand basal area is not affected greatly because the smaller stems contribute very little to total basal area. The model does fairly well in projecting the number of large stems, which is crucial to obtaining reasonable values of total basal area. If accuracy in simulating the number of small stems is desired, the simulated ingrowth and survivorship of stems must be evaluated to guide model revisions (e.g.Wehrli et al., 2005). Further work on the simulation of processes regulating small stems should increase the accuracy of total tree density as well as size-class structure.

Summary

An individual-based model of forest dynamics (FORCLIM) was tested for its ability to simulate forest composition and structure in the Pacific Northwest region of North America. Simulation results across gradients of climate and disturbance were compared to forest survey data from several vegetation zones in western Oregon.

General biogeographic patterns in forest composition and structure are reproduced by the model. The basal area of dominant species is approximated well. Also, the decline in total basal area and mean tree height along a gradient from wet, maritime to dry, continental environments is captured by the model. These trends are associated with compositional changes along the same gradient from very tall species (e.g. *Pseudotsuga*) to species with diminished stature (e.g. *Pinus*). Simulations with stand-replacing disturbances and partial-stand disturbances give results that match several composition and structure variables measured in actual forests along this gradient. However, for some structural variables (e.g. total tree density) none of the simulations give accurate results. Simulated tree density values tend to underestimate the abundance of small stems. Stem-density structure of simulated stands is a shortcoming of this version of the FORCLIM model (cf. Risch et al., 2005; Wehrli et al., 2005). By contrast, the model is quite good at projecting tree species composition, basal area, biomass and stand height in the forests of western Oregon. It is also able to project generalized size-class structure patterns. Although the model captures major compositional changes along climatic gradients quite well, the simulation of physical stand structure involving stem size and density is an area requiring further work.

References

Acker, S.A., McKee, W.A., Harmon, M.E. & Franklin, J.F. 1998. Long-term research on forest dynamics in the Pacific Northwest: a network of permanent plots. Forest biodiversity in North, Central, and South America and the Carribbean. (ed. By F. Dallmeier & J.A. Comiskey), pp. 93-106. Parthenon, Washington, D.C.

Agee, J.K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C.

Bonan, G.B. & Sirois, L. 1992. Air temperature, tree growth, and the northern and southern range limits to *Picea mariana*. J. Veg. Sci. 3:495-506.

Botkin, D.B. 1992. Forest dynamics: an ecological model. Oxford University Press, New York.

Botkin, D.B., Janak, J.F. & Wallis, J.R. 1972. Some ecological consequences of a computer model of forest growth. J. Ecol. 60:849-872.

Bugmann, H. 1994. On the ecology of mountainous forests in a changing climate: a simulation study. Ph.D. Dissertation, ETH, Swiss Federal Institute of Technology, Zurich Switzerland.

Bugmann, H.K.M. 1996. A simplified forest model to study species composition along climate gradients. Ecology 77: 2055-2074.

Bugmann, H. 2001. A review of forest gap models. Climatic Change 51:259-305.

Bugmann, H., & Cramer, W. 1998. Improving the behavior of forest gap models along drought gradients. For. Ecol. Manage. 103:247-263.

Bugmann, H.K.M., & Solomon, A.M. 1995. The use of a European forest model in North America: a study of ecosystem response to climate gradients. J. Biogeogr. 22: 477-484.

Bugmann, H.K.M., & Solomon, A.M. 2000. Explaining forest composition and biomass across multiple biogeographical regions. Ecol. Appl. 10:95-114.

Busing, R.T. 2004. A vegetation database for western Oregon. U.S. Geological Survey Open File Report OF 2004-1249.

Busing, R.T., & Solomon, A.M. 2004. A comparison of forest survey data with forest dynamics simulators FORCLIM and ZELIG along climatic gradients in the Pacific Northwest. U.S. Geological Survey Scientific Investigations Report 2004-5078.

Cumming, S.G. & Burton, P.J. 1996. Phenology-mediated effects of climate change on some simulated British Columbia forests. Climatic Change 34:213-222.

Dale, V.H. & Franklin, J.F. 1989. Potential effects of climate change on stand development in the Pacific Northwest. Can. Jour. Forest Res. 19:1581-1590.

Daubenmire, R. 1978. Plant geography. Academic Press, New York.

Franklin, J.F., & Dyrness, C.T. 1988. Natural vegetation of Oregon and Washington. Oregon State Univ. Press, Corvallis, OR.

Franklin, J.F., & Halpern, C.B. 2000. Pacific Northwest forests. North American terrestrial vegetation (ed. By M.G. Barbour & W.D. Billings), pp. 123-159. Cambridge University Press, New York.

Franklin, J.F., & Hemstrom, M.A. 1981. Aspects of succession in the coniferous forests of the Pacific Northwest. Forest succession: concepts and application (ed. By D.C. West, H.H. Shugart & D.B. Botkin), pp. 212-229. Springer-Verlag, New York.

Fujimori, T., Kawanabe, S., Saito, H., Grier, C.C., & Shidei, T. 1976. Biomass and primary production in forests of three major vegetation zones of the northwestern United States. Jour. Japanese Forestry Soc. 58: 360-373.

Gates, D.M. 1993. Climate change and its biological consequences. Sinauer Associates, Sunderland, Massachusetts.

Gholz, H.L. 1982. Environmental limits on aboveground net primary production, leaf area, and biomass in vegetation zones of the Pacific Northwest. Ecology 63: 469-481.

Harcombe, P.A. 1986. Stand development in a 130-year-old spruce-hemlock forest based on age structure and 50 years of mortality data. For. Ecol. Manage. 14:41-58.

Husch, B., Beers, T.W. & Kershaw, J.A. 2003. Forest mensuration. Wiley, Hoboken, New Jersey.

Iman, R.L. & Conover, W.J. 1987. A measure of top-down correlation. Technometrics 29: 351-357.

Kienast, F. 1987. FORECE—a forest succession model for southern central Europe. Oak Ridge National Laboratory, Oak Ridge, Tennessee, ORNL/TM-10575.

Loehle, C. & LeBlanc, D. 1996. Model-based assessments of climate change effects on forests: a critical review. Ecol. Modelling 90:1-31.

Lugo, A.E., Brown, S., Dodson, R., Smith, T.M. & Shugart, H.H. 2000. The Holdridge life zones of the conterminous United States in relation to ecosystem mapping. Journal of Biogeography 26:1025-1038.

Max, T.A., Schreuder, H.T., Hazard, J.W., Oswald, D.D., Teply, J. & Alegria, J. 1996. The Pacific Northwest region vegetation and inventory monitoring system. USDA Forest Service Research Paper PNW-RP-493, Portland, OR.

Pacala, S.W. & Hurtt, G.C. 1993. Terrestrial vegetation and climate change: integrating models and experiments. Biotic interactions and global change (ed. By P.M. Kareiva, J.G. Kingsolver, & R.B. Huey), pp. 57-74. Sinauer Associates, Sunderland, Massachusetts.

Reynolds, J.F., Bugmann, H. and Pitelka, L.F. 2001. How much physiology is need in forest gap models for simulating long-term vegetation response to global change? Challenges, limitations and potentials. Climatic Change 51: 541-557.

Risch, A.C., Heiri, C., and Bugmann, H. 2005. Simulating structural forest patterns with a forest gap model: a model evaluation. Ecol. Modelling 181:161-172.

Schenk, H.J. 1996. Modeling the effects of temperature on growth and persistence of tree species: a critical review of tree population models. Ecol. Modelling 92:1-32.

Shugart, H.H. 1984. A theory of forest dynamics. Springer-Verlag, NY.

Shugart, H.H. & West, D.C. 1977. Development of an Appalachian deciduous forest succession model and its application to assessment of the impact of the chestnut blight. Jour. Environ. Manage. 5:161-179.

Sternes, G.L. 1960. The climate of Oregon. Climates of the states, Vol. 2 (NOAA), pp. 841-860. Water Information Center, New York.

Thornthwaite, C.W. & Mather, J.R. 1957. Instructions and tables for computing potential evapotranspiration and the water balance. Publ. Climatol. 10:183-311.

Thorson, T.D., Bryce, S.A., Lammers, D.A., Woods, A.J., Omernik, J.M., Kagan, J., Pater, D.E., & Comstock, J.A. 2002. Ecoregions of Oregon. (2 sided color poster with map, descriptive text, summary tables, and photographs). U.S. Geological Survey, Reston, VA. Scale 1:1,350,000.

Urban, D.L., Harmon, M.E. & Halpern, C.B. 1993. Potential response of Pacific Northwestern forests to climatic change, effects of stand age and initial composition. Climatic Change 23:247-266.

Wehrli, A., Zingg, A., Bugmann, H. & Huth, A. 2005. Using a forest patch model to predict the dynamics of stand structure in Swiss mountain forests. For. Ecol. Manage. 205:149-167.

Whittaker, R.H. 1966. Forest dimensions and production in the Great Smoky Mountains. Ecology 47:103-121.

Zolbrod, A.N. & Peterson, D.L. 1999. Response of high-elevation forests in the Olympic Mountains to climatic change. Can. J. For. Res. 29:1966-1978.