



A Comparison of Forest Survey Data with Forest Dynamics Simulators FORCLIM and ZELIG along Climatic Gradients in the Pacific Northwest



Scientific Investigation Report 2004-5078

U.S. Department of the Interior
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By Richard T. Busing and Allen M. Solomon

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A Comparison of Forest Survey Data with Forest Dynamics Simulators FORCLIM and ZELIG along Climatic Gradients in the Pacific Northwest

By Richard T. Busing and Allen M. Solomon

Abstract

Two forest dynamics simulators are compared along climatic gradients in the Pacific Northwest. The ZELIG and FORCLIM models are tested against forest survey data from western Oregon. Their ability to generate accurate patterns of forest basal area and species composition is evaluated for series of sites with contrasting climate. Projections from both models approximate the basal area and composition patterns for three sites along the elevation gradient at H.J. Andrews Experimental Forest in the western Cascade Range. The ZELIG model is somewhat more accurate than FORCLIM at the two low-elevation sites. Attempts to project forest composition along broader climatic gradients reveal limitations of ZELIG, however. For example, ZELIG is less accurate than FORCLIM at projecting the average composition of a west Cascades ecoregion selected for intensive analysis. Also, along a gradient consisting of several sites on an east to west transect at 44.1°N latitude, both the FORCLIM model and the actual data show strong changes in composition and total basal area, but the ZELIG model shows a limited response. ZELIG does not simulate the declines in forest basal area and the diminished dominance of mesic coniferous species east of the Cascade crest. We conclude that ZELIG is suitable for analyses of certain sites for which it has been calibrated. FORCLIM can be applied in analyses involving a range of climatic conditions without requiring calibration for specific sites.

Introduction

Two ecological simulators of forest dynamics in the Pacific Northwest are ZELIG (Urban 1993) and FORCLIM (Bugmann 1994). Both are individual-based “gap models” (sensu Shugart 1984) designed for simulation of forest dynamics at multiple spatial and temporal scales (e.g. Smith and Urban 1988). The ZELIG model has been modified and applied for over a decade to project stand and landscape dynamics of forests in response to various human and natural disturbances, including tropospheric ozone (Urban et al. 1993; Hansen et al. 1995; Miller and Urban 1999; Weinstein 2001; Busing and Garman 2002; Garman et al. 2003). The FORCLIM model has been applied recently to project forest

stand composition across regional climatic gradients in the Pacific Northwest, and earlier, in eastern North America and western Europe (Bugmann and Solomon 1995, 2000).

The two models have several contrasting features. ZELIG has enhanced spatial complexity, allowing consideration of stand and landscape structure (Smith and Urban 1988; Urban 1993). The simulation of up to several hundred interacting plots at once enables ZELIG to address landscape-level processes such as seed transport and fire spread. FORCLIM, on the other hand, has enhanced consideration of site and climatic effects on tree species performance (Bugmann 1994). Current versions of FORCLIM are especially suitable for regions with strong seasonal contrasts in climate (e.g. winter precipitation alternating with summer drought), such as the Pacific Northwest (Bugmann and Solomon 2000), by virtue of mechanistic routines to simulate impacts of growing season drought on tree growth and survival.

The objective of this report is to provide readers with the information they need to choose one or the other model for the application they are planning. It focuses on how ZELIG and FORCLIM perform along regional environmental gradients in western Oregon. We emphasize the ability of the models to reproduce patterns of forest composition and structure along climatic gradients. We believe that an important capability of the models in this regard is their simulation of forests where forests grow, and forest absence in places forests do not now grow. Also, where forests grow, the models should simulate dominance by the actual dominant species (as measured in field plot surveys and studies), the approximate order of species importance, and total stand biomass that resembles estimates from field data.

Methods

Models and Field Data

The FORCLIM model version 2.9 was employed using 18 species (Bugmann 1996). The species set included all common dominant trees species in western Oregon north of 43° N latitude. For reasons outlined below, certain FORCLIM simulations used only 8 species.

A version of the ZELIG model was applied that had been modified and tested using a set of 8 tree species in the west-

¹ Ten other species, including some potential dominants (e.g. *Picea sitchensis* and *Pinus ponderosa*) were added to create a larger pool of species. For the set of species added, growth scaling constants (G) were set equal to four times the value used in FORCLIM. Rescaling of these constants was necessary because the two models have somewhat different growth equations, despite their use of Moore's (1989) formulation for tree growth. Following tests with even further increases in the growth scaling constants and removal of competing species, it was concluded that environmental constraints as modeled in ZELIG must be limiting the growth of some of these new species.

A Comparison of Forest Survey Data with Forest Dynamics Simulators

ern Cascade Range of Oregon. Using the personal-computer program for this model, known as PNWGAP version 1.0 (Garman 2003), we simulated forest dynamics with a set of 18 tree species common to western Oregon and Washington. This required adding 10 tree species to the ZELIG simulations. However, ZELIG model runs using all 18 species were distinctive in that several of the 10 new species had poor growth and survival. This problem persisted despite several attempts to enhance performance of certain species¹. Hence, as mentioned below, we also ran simulations in which both ZELIG and FORCLIM contained only the 8 species common to both, in order to generate valid comparisons between the two models. However, the emphasis in this report is not on how they compare to each other, but rather on the degree to which each model approximates measured vegetation. This latter assessment demands that each model be run with its optimum configuration, whether that involves 8 or 18 species.

Other versions of ZELIG were considered for this analysis, but concerns over species parameterization difficulties led to the selection of the PNWGAP version. Attempts to parameterize the version of ZELIG used primarily in the Appalachian Mountain region were unsuccessful despite the use of values for species variables based on parameterization guidelines (Laurence et al. 2001). A major difficulty was that Douglas-fir (*Pseudotsuga menziesii*), a very common dominant species in the Pacific Northwest, was an uncommon species at any successional stage simulated. Under-representation of *Pseudotsuga* also occurred in previous simulation work by independent researchers attempting to apply earlier versions of ZELIG to western Oregon (Garman and Hansen 1991; Urban et al. 1993). By contrast, *Pseudotsuga* is a successional dominant in simulations by the PNWGAP version of ZELIG. This version has been adapted to, and tested for simulation of, forest composition in the western Cascade Range of central Oregon. Considering the foregoing, and that this version has been under development and testing for the past 15 years, we believe it represents the optimum available configuration for ZELIG in the western Oregon tests we describe below.

Parameterization of ZELIG

Parameters for the eight species in Garman's PNWGAP program were not altered. These species included Pacific silver fir (*Abies amabilis*), noble fir (*Abies procera*), Douglas-fir (*Pseudotsuga menziesii*), western red cedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), bigleaf maple (*Acer*

macrophyllum), red alder (*Alnus rubra*) and mountain hemlock (*Tsuga mertensiana*). Growing-degree-day limits (DDMIN and DDMAX) followed the values published in Urban et al. (1993). The inseedling parameter SEED was set equal to 3 for the additional 10 species. This is an intermediate level of inseedling. None of the new species was assigned a mineral soil requirement for regeneration. For each new species, adult reproductive size was set at 20, which is the minimum diameter (cm dbh) of seed producing trees. Simulation sites had silt loam soils with a depth of 1m, a field capacity of 43.7 cm/m and a wilting point of 16.3 cm/m per layer. Only monthly mean precipitation and temperature were varied among sites.

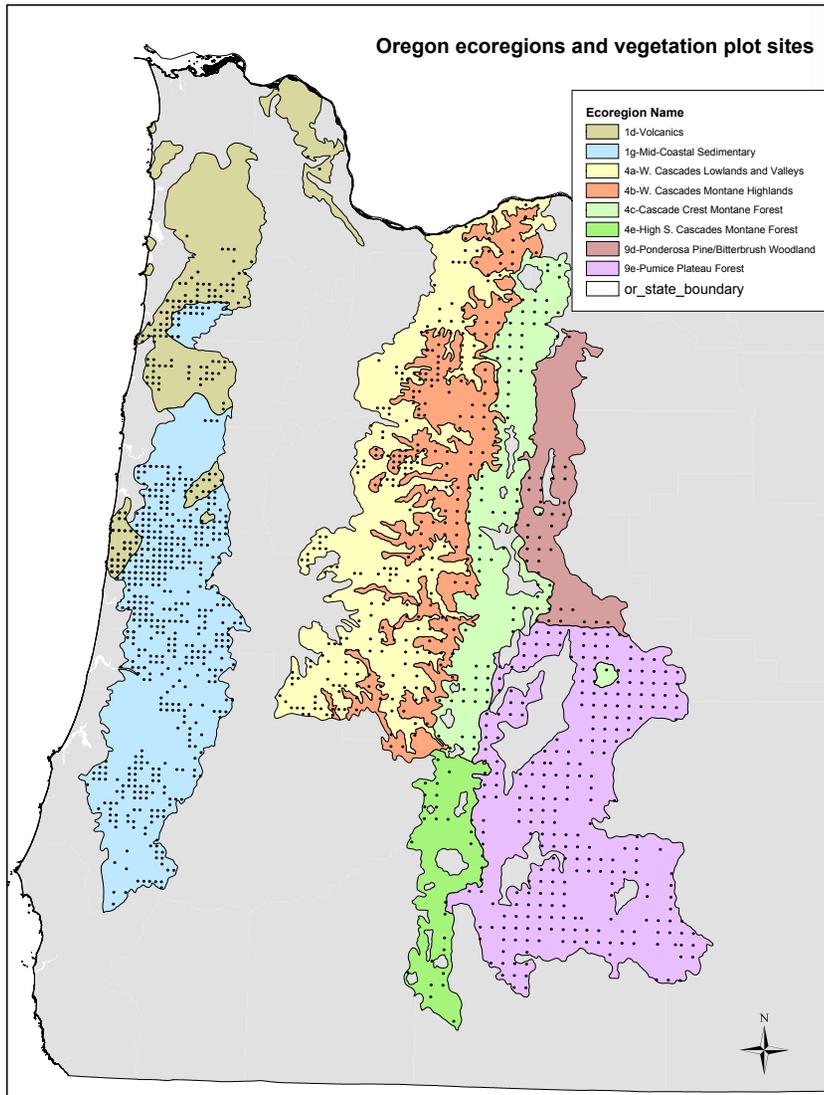
Parameterization of FORCLIM

Version 2.9 of the FORCLIM model (Bugmann 1996, Bugmann and Solomon 2000) was used with 18 species (interior region subspecies of *Pseudotsuga menziesii* and lodgepole pine/shore pine (*Pinus contorta*) were included, making a total of 20 taxa simulated). Species parameters generally matched those in Bugmann (1996), derived as described by Bugmann and Solomon (2000)². However, certain parameterizations were revised following examination of species parameters for drought tolerance and growing-degree-day minima for each species. Comparison of the old parameters to values in recently published climatic data sets associated with species' ranges (Thompson et al. 2000 a, b) revealed some discrepancies. In cases where the Thompson et al. data clearly did not agree with the parameter value of Bugmann (1996), new values provided by Thompson et al. were assigned. Specifically, the drought tolerance parameters (percent of growing season days with soil moisture below the wilting point) of *Abies amabilis* and *Abies procera* were reduced from 0.4 and 0.3 to 0.2 and 0.25, respectively. The DDMIN values (minimum growing degree days) of grand fir (*Abies grandis*), *Abies procera*, *Alnus rubra*, and Engelmann spruce (*Picea engelmannii*) (705, 821, 705, and 488, respectively) also were reduced (to 600, 550, 600 and 400, respectively).

Simulation sites were assumed to have a slope aspect factor of 0, water holding capacity of 20% (i.e., 20 cm/m) and a water table of 10 m. Soils were assumed to be fertile. Only monthly mean precipitation and temperature were varied among sites.

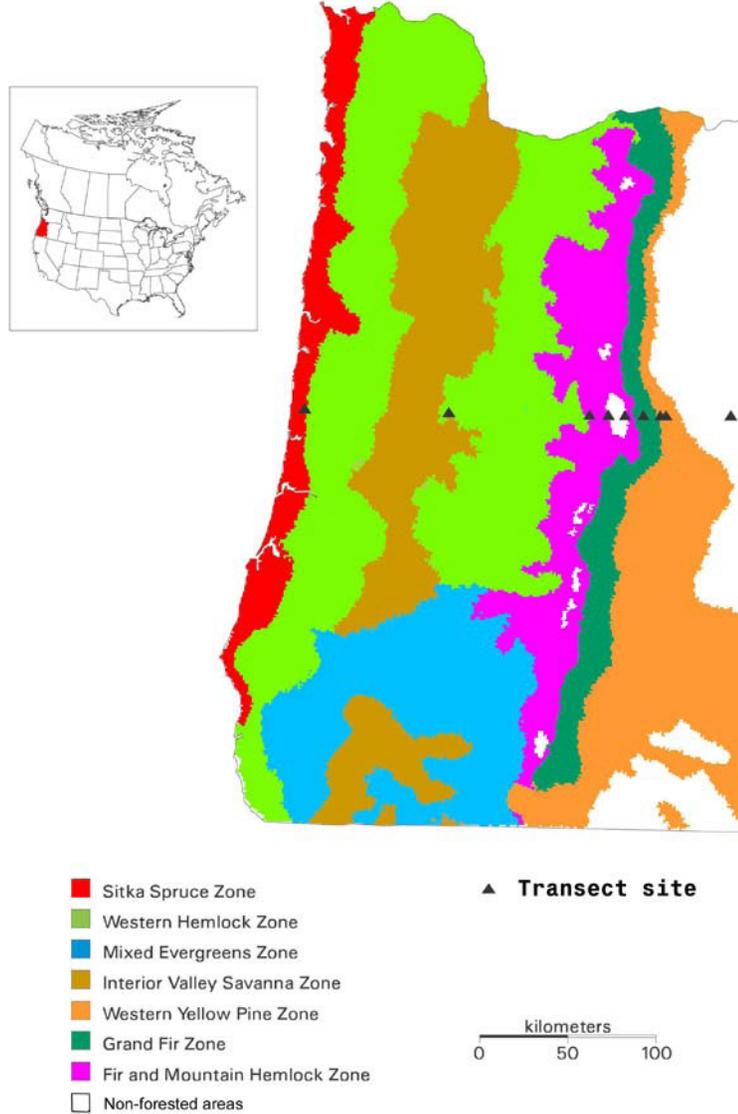
FORCLIM is implemented primarily in MODULA2 computer code. Previously published results are from the MODULA2 program (e.g. Bugmann and Solomon 2000).

² Climatic parameters were estimated based on overlays of tree distribution maps by maps of bioclimatic indices (minimum degree-days kDDMin, min. and max. winter temperature tolerances kWITN, kWITX, and drought tolerance kDrT). These estimation procedures yielded congruent values that resulted in plausible simulation results except for the minimum degree-day and drought tolerance parameters. Steep climatic gradients were problematic here. For example, the initial estimates of the kDDMin parameter obtained from overlaying distribution maps (Little 1971) on maps of the degree-day sums yielded estimates that had a resolution of no more than 200 °C-days. We refined those estimates from the ranking of species' minimum temperature requirements in Franklin & Dyrness (1973, p. 161). The estimates of the kDrT parameter obtained from overlays of distribution maps with maps of the simulated drought index values, uDrE and uDrD, matched the ranking of the species by Franklin & Dyrness (1973, p. 130). However, several species had been assigned only slightly different drought indices by the crude means applied, although according to Franklin and Dyrness (1973) they behave rather differently toward soil moisture. Therefore, we modified the kDrT parameters of *Alnus rubra*, *Acer macrophyllum*, *Pinus ponderosa*, and *Abies grandis* accordingly. See Bugmann & Solomon (2000) for additional details and references.



A

Simulation modelling site transect and major vegetation zones of western Oregon



B

Figure 1. Maps of Oregon, including (A) locations of CVS forest survey plots used within Level IV Ecoregions, and (B) locations of nine sites along the geographic gradient transect. The eight ecoregions include coastal Volcanics (1d), Mid-Coastal Sedimentary (1g), Western Cascades Lowlands and Valleys (4a), Western Cascades Montane Highlands (4b), Cascade Crest Montane Forest (4c), High Southern Cascades Montane Forest (4e), Ponderosa Pine—Bitterbrush Woodland (9d), and Pumice Plateau (9e). For the transect sites, proximate CVS forest plots were used in comparisons of simulations to actual vegetation.

A Comparison of Forest Survey Data with Forest Dynamics Simulators

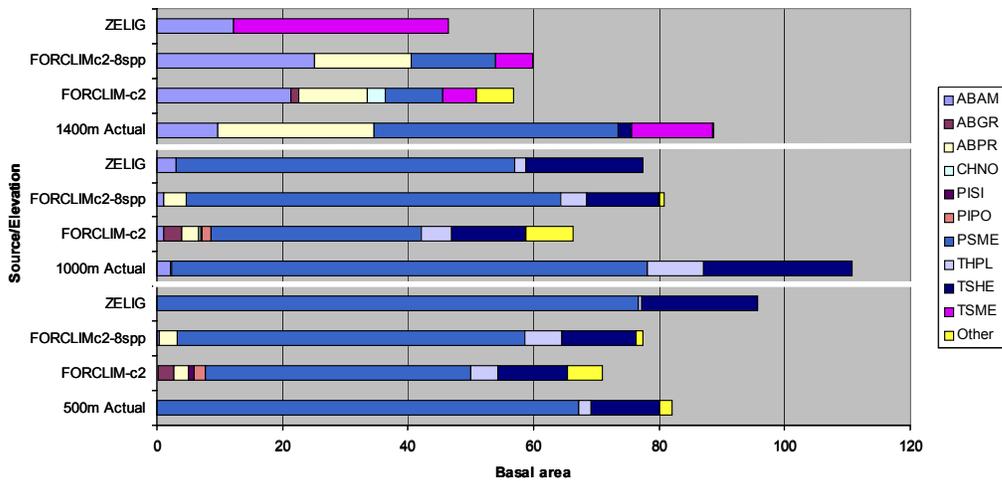


Figure 2. Basal area by species, including values simulated by FORCLIM and ZELIG, and values from stands at H.J. Andrews Experimental Forest, western Cascade Range. FORCLIM results include the normal 18-species version and an eight-species version for direct comparison to ZELIG simulations. The eight-species version is not used for other FORCLIM simulations in this report unless so noted. The four-letter species codes consist of the first two letters of the genus and of the species names, respectively.

However, unless noted otherwise, a C version of the program running under the UNIX operating system and developed for USEPA (Dodson 1997), was used for the simulations herein.

Types and Sources of Field Data

Forest plot data from recent ecological surveys and studies in western Oregon were used for evaluations of the models. The data sets include ecological survey data from plots on a grid extending across federal lands, and stand data from plots in selected sites at H.J. Andrews Experimental Forest in the Cascade Range.

The ecological survey data included 2323 forest stands in western Oregon that were 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 (Fig. 1A). A five-subplot design covered a 1-ha area for tree stratum data collection at each plot site. Measurements on live trees included diameter at breast height, canopy height and, for selected individuals at most sites, tree age. We selected sites in which all five subplots were inventoried and tree age data were collected.

Our analyses with the Current Vegetation Survey data included all live trees >7.6 cm dbh. We calculated basal area for selected dominant species and for all species combined. Stand age 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).

Another set of long-term research plots in old growth forests, known as the H.J. Andrews Experimental Forest reference stands, was also used (Acker et al. 1998; Garman and

Hansen 1991). A total of 25 stands representing old (>400 yr), well-developed forests along the elevation gradient in the western Oregon Cascade Range were selected for analysis. For the comparisons with simulated data, stands were grouped into one of three elevation classes: 1) ca. 500 m (n=11); 2) ca. 1000 m (n=9); and 3) ca. 1400 m (n=5).

Model Tests

Models were tested for their ability to reproduce compositional and structural patterns observed in the field. All simulations were initiated on bare ground and were run to match measured ages of actual stands. Simulated basal area means were compared among simulations and with actual data. In comparisons with the reference stands data at H.J. Andrews Experimental Forest in the western Cascade Range (Garman and Hansen 1991) size-class distributions were examined as well.

Actual data from the survey plots located on forested lands in western Oregon representing vegetation types occurring north of 43° N latitude were used in another set of tests. Two separate vegetation classifications were applied: a transect across the commonly applied forest vegetation zones of Franklin and Dyrness (1988) (Fig. 1B); and (primarily for FORCLIM comparisons to actual vegetation) Omernik's Ecoregion IV classification (Thorsen et al. 2002) (Fig. 1A), which emphasizes physiographic and climatic as well as vegetation classification variables. Both of these classifications are commonly used and understood, though each primarily by workers in different disciplines. Comparisons applying both systems provide readers with the opportunity to picture the forests that the models are simulating in terms that they understand best.

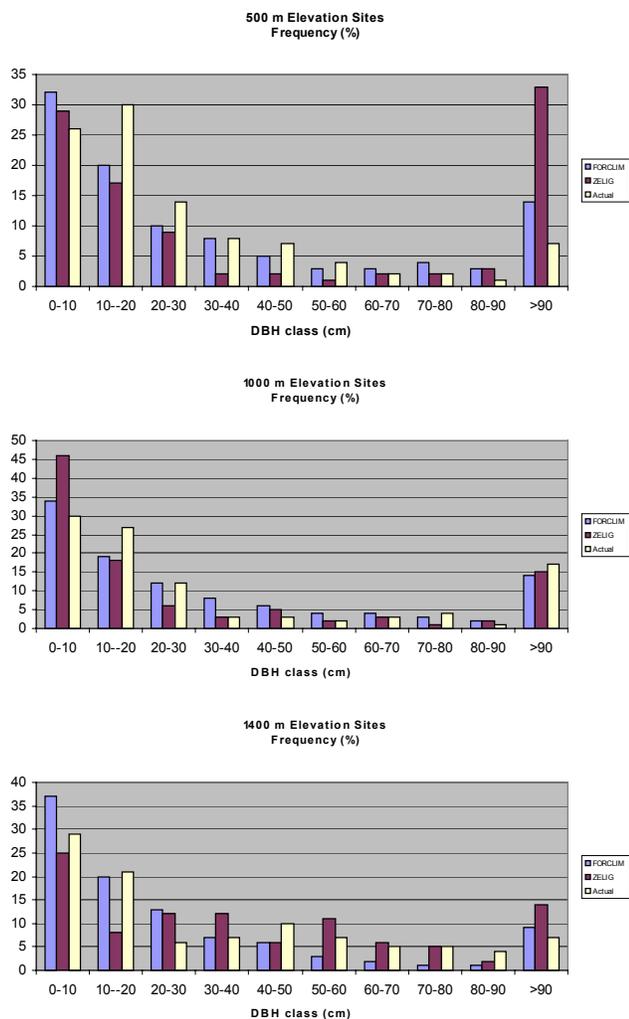


Figure 3. Percent frequency by diameter class of trees at H.J. Andrews sites (A) near 500 m elevation, (B) near 1000 m elevation, and (C) near 1400 m elevation. Values simulated by the ZELIG and FORCLIM models are provided for comparison.

West Cascades Test

Both models were run at three sites along the elevation gradient (~500, 1000, & 1400 m) at H.J. Andrews Experimental Forest (Fig. 1B). Both ZELIG and FORCLIM had previously been run at these sites because comprehensive vegetation data for comparison to simulation output was available there. These sites are actually composites of many measured plots at each elevation, retrieved and formatted from the H. J. Andrews Long Term Ecological Research (LTER) database by Garman and Hansen (1991). Basal area means for each species and for all species combined were compared at each site (Fig. 2). Diameter distributions for all species combined in diameter classes, from forest surveys (10 cm dbh), FORCLIM (18 species) and ZELIG (8 species) simulations, were compared using percent frequency by diameter class (Figs. 3A, 3B, 3C, respectively).

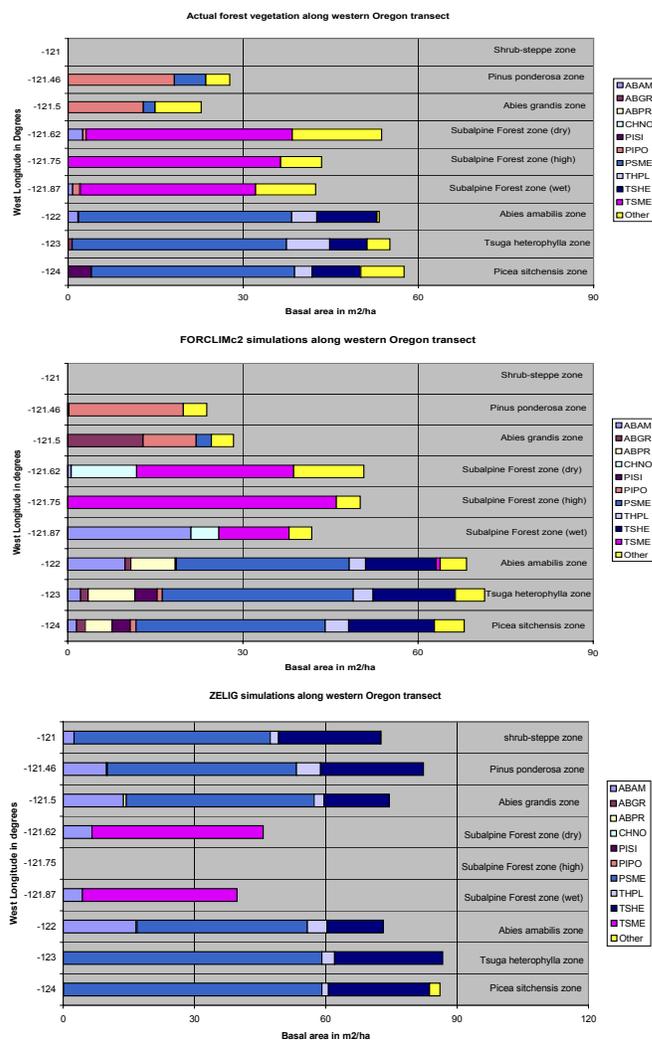


Figure 4. Basal area by species along a geographic transect of western Oregon sites from dry, continental treeless shrub-steppe, across cold subalpine forests to wet maritime coastal forests. Results include (A) CVS forest plot data, (B) FORCLIM simulation output, and (C) ZELIG simulation output. The four-letter species codes consist of the first two letters of the genus and species names.

Geographic Transect Test

A geographical climate gradient in western Oregon was described and analyzed by Bugmann and Solomon (2000). This gradient was composed of a set of sites along a west-east transect from the coast to the steppe in central Oregon (at 44.13° N), approximately as described by Franklin and Dyrness (1988). For the comparative analyses, we selected nine of the 27 sites along this transect (See Fig. 1B) that were simulated by Bugmann and Solomon (2000). The nine test sites included wet, coastal forests, mesic and zeric montane forests, cold subalpine forests, and dry, treeless steppe. Basal area means for each species and for all species combined from CVS data (several to many CVS plots combined per site) and from FORCLIM and ZELIG simulations, were compared at each site (Figs. 4A, 4B, 4C, respectively).

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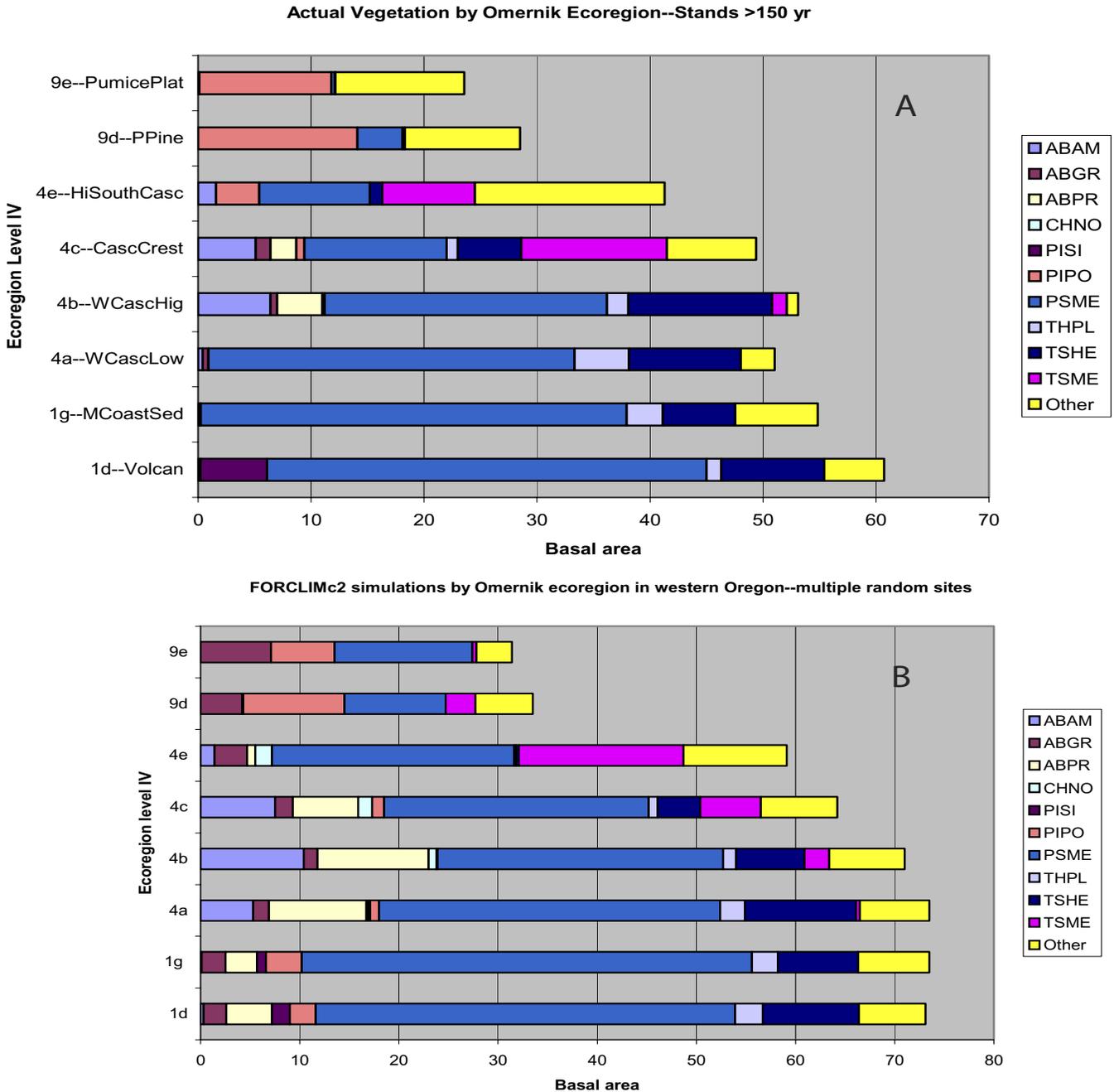


Figure 5. Basal area (m^2/ha) by species in Ecoregion Level IV sites from (A) CVS forest data, and (B) FORCLIM simulation output. The four-letter species codes consist of the first two letters of the genus and species names.

Forested Ecoregion Test

Eight ecoregions from the Omernik classification (level IV; Thorson et al. 2002) in western Oregon were selected based on the number of field plots (>12 plots) confirmed to represent older stands (age >150 yr) in each level IV category. Ecoregions at low elevations centered south of 43° N latitude (i.e., the Siskiyou) were excluded because they contained dominant species that are not currently considered in either FORCLIM or ZELIG. Unlike the other tests, this one segregated vegetation by substrate features as well as climate,

permitting the examination of vegetation composition and biomass patterns conforming to soil texture and nutrient status.

The eight ecoregions are listed and mapped in Figure 1A. The climatic regime of each ecoregion, extracted from the 4-km climate data set (Dodson 1997), was assembled from climate data at multiple randomly selected CVS plot sites ($n = 10$ to 20). A FORCLIM simulation was run for each of these sites. Results were pooled by ecoregion (Figs. 5A, 5B).

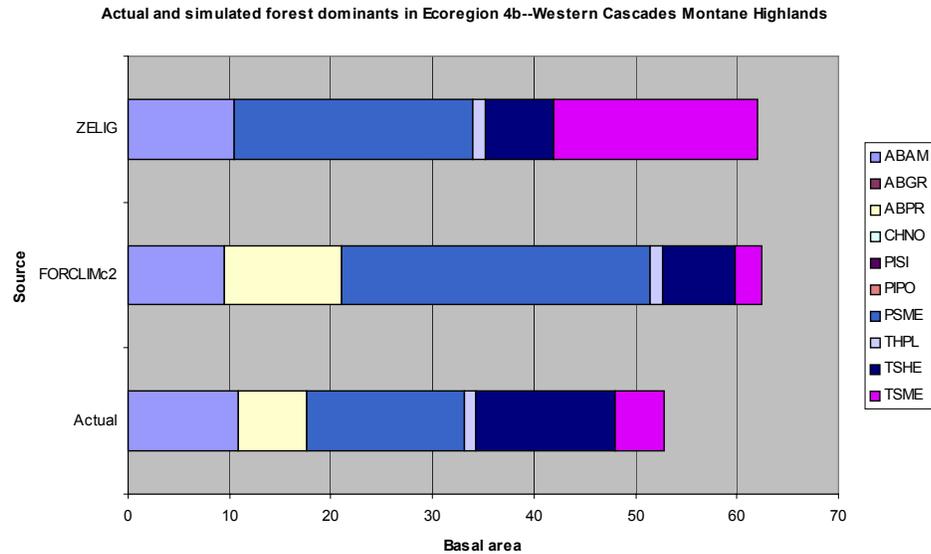


Figure 6. Basal area (m²/ha) by species in Ecoregion 4b (Western Cascades Highlands), including CVS forest data, FORCLIM simulation output, and ZELIG simulation output. The four-letter species codes consist of the first two letters of the genus and species names.

Actual Vegetation along Test Gradients

Actual vegetation along the two broad test gradients and the ecoregions was documented from the field data. For the geographic transect gradient, CVS plots having trees known to be at least 150 years old were selected from a belt between 43.13 and 45.13° N latitude. For each point along the transect, plot sites with similar longitude and within 500 ft elevation of the transect point were analyzed for mean species basal area and total basal area. Mean age was also calculated. For the forested ecoregions, these values were generated for each ecoregion. Plots were excluded if they had basal area <10 m² ha⁻¹ (indicating lack of closed canopy) or no evidence of trees >150 years old (indicating early successional forests).

Species Pool Effects

All of the FORCLIM and ZELIG tests involved 18 species, and were repeated with only the eight tree species from the version of ZELIG calibrated by Garman (1999). All other species were excluded from the simulations so that results could be evaluated without the effects of additional FORCLIM species, which had not been calibrated for the two models. Ten forest sites (>150 yr) were randomly selected for the comparison. FORCLIM and ZELIG simulations were run for each of these sites. Actual and simulated data for dominant tree species were summarized for the ecoregion (Fig. 6).

Unlike FORCLIM simulations, running ZELIG at these sites required a separate parameterization for model runs at each site within each ecoregion (i.e., 8 ecoregions X 10-20 sites). To reduce the time required to prepare for the ecoregion comparisons using both models, we ran only a single set of FORCLIM and ZELIG simulations, covering the Western Cascades Montane Highlands ecoregion (class 4b). All forest

dominants in this ecoregion have been tested previously for reasonable growth in the ZELIG model, making this ecoregion optimal for ZELIG in a comparison of ZELIG. We note that when simulation output is compared to actual vegetation, at least in FORCLIM, model performance is degraded by exclusion of species known to grow in the area being modeled (Bugmann et al. 2001). Hence, FORCLIM with eight species is likely to be considerably less accurate than FORCLIM simulations that include the missing species. An additional disadvantage of species exclusion is that it reduces the identifiable differences among the data sets by leaving out signature species (e.g., ponderosa pine [*Pinus ponderosa*] in dry eastern forests, Sitka spruce [*Picea sitchensis*] in wet coastal forests). However, species exclusion does have the virtue of reducing the potential for unwanted species calibration effects, which apply, to ZELIG but not to FORCLIM (species of which are not calibrated by site). It also allows evaluation of model sensitivity to species pool selection.

Results

Actual Vegetation Patterns

The field data on forest vegetation show somewhat subtle compositional changes along environmental gradients. Major geographic trends in composition along the geographic transect at 44.1° N latitude from the coast to the dry steppe are evident (Fig. 4A). Near the coast (-124° W longitude), forests are dominated by *Pseudotsuga*, *Tsuga heterophylla* and *Picea sitchensis*. In the Cascade Range (-123° and -122° W longitude), *Pseudotsuga*, *Tsuga heterophylla* and *Thuja plicata* dominate. In the high Cascades (-121.87° to -121.62° W longitude) *Tsuga mertensiana* dominates sites warm enough

A Comparison of Forest Survey Data with Forest Dynamics Simulators

Table 1. Similarity of species composition simulated by each model to actual species composition for (A) west Cascades sites, (B) western Oregon transect sites, and (C) forested ecoregions. Similarity is measured with Sorensen's quantitative index using species basal area.

[(A) H.J. Andrews LTER comparisons]

Site	Actual vs. FORCLIM	Actual vs. ZELIG
H.J. Andrews 500 m	0.746	0.884
H.J. Andrews 1000 m	0.579	0.814
H.J. Andrews 1400 m	0.488	0.336

[(B) Western Oregon transect at 44.1° N comparisons]

Longitude	Forest Zone	Actual vs. FORCLIM	Actual vs. ZELIG
-124	<i>Picea sitchensis</i>	0.828	0.632
-123	<i>Tsuga heterophylla</i>	0.745	0.649
-122	<i>Abies amabilis</i>	0.738	0.835
-121.87	<i>Tsuga mertensiana</i>	0.397	0.750
-121.75	<i>Tsuga mertensiana</i>	0.477	0
-121.62	<i>Tsuga mertensiana</i>	0.757	0.761
-121.5	<i>Abies grandis</i>	0.524	0
-121.46	<i>Pinus ponderosa</i>	0.870	0.098
Mean and Standard Deviation	All	0.667+0.176	0.466+0.365

[(C) Ecoregion comparison]

Region	Actual vs. FORCLIM	Actual vs. ZELIG
Ecoregion 4b	0.740	0.655

to permit tree growth. On the lower, eastern slopes of the Cascades (-121.5° W longitude) *Pinus ponderosa* dominates and total basal area diminishes. Forest is absent at the eastern-most site (-121° W longitude).

Deciduous species (e.g. *Acer macrophyllum* and *Alnus rubra* in the mesic low-elevation sites) and subalpine conifers (e.g. *Picea engelmannii* and *Abies lasiocarpa* in the high-elevation sites) occur in the CVS plots sporadically, and are assigned to the “other” species category.

Similar compositional changes were evident in the series of eight ecoregions from wet, coastal forests to dry forests of central Oregon (Fig. 5A). However, ecoregion summaries also revealed the potential diversity of tree species on the landscape in a given ecoregion. For example, in the high elevation ecoregions along the Cascade crest, the landscape is not dominated exclusively by one or two tree species.

Simulated Vegetation Patterns

Western Cascade Range

Performance of the FORCLIM and ZELIG models at three elevations (500, 1000 & 1400 m) in the western Oregon Cascades (H.J. Andrews Experimental Forest) may be acceptable for most purposes to which the models would be applied. Both ZELIG and FORCLIM projected dominance by *Pseudotsuga* and *Tsuga heterophylla* at the 500 and 1000 m elevation sites, as observed in the actual reference stands at these two sites (Fig. 2). At the high-elevation site (1400 m), however, there were obvious discrepancies between species composition measured and that simulated by both models. The actual forest composition was *Pseudotsuga*—*Abies procera*—*Tsuga mertensiana*. FORCLIM simulated a forest of *Abies amabilis*—*Abies procera*—*Pseudotsuga*. ZELIG produced a

Tsuga mertensiana—*Abies amabilis* forest. FORCLIM underestimated the amount of *Pseudotsuga* at the upper site where ZELIG overestimated the amount of *Tsuga mertensiana* and greatly underestimated the amount of *Pseudotsuga* and *Abies procera*.

Quantitative indices of similarity in species composition were used to further evaluate model performance. Sørensen's Index of Similarity [a quantitative Coefficient of Community (CoC); Magurran 1988] indicates that ZELIG simulations are particularly accurate at the 500 and 1000 m sites, and that FORCLIM is similarly accurate at the 500 m sites, but less so at the 1000 m sites (Table 1A). Although the CoC indicates that FORCLIM is considerably more accurate at 1400 m than is ZELIG, neither model appears to be acceptably correct, assuming the measured values are characteristic of the forests at these high elevations.

However, there is some reason to question whether these specific high- and mid-elevation measurements are indeed representative of upper-elevation forests. It is noteworthy that the data from actual reference stands representing these two sets of sites contained much higher basal area than did most of the simulations (Fig. 2). This may result from bias towards recording well-developed stands during the selection of these study plot sites in the field. On average, the CVS vegetation survey plots covering these same high elevations do not contain such high basal area (e.g. Figs. 4A, 5A, 6A) even though sites with human disturbance are excluded. Hence, the actual total basal area (if not the species basal area) values from the reference stands must be interpreted cautiously, as they do not appear to represent randomly selected sites.

Size-class structures (or diameter distributions) of the actual plots at these three sites all had the typical pattern of decreasing stem densities with stem size (Figs. 3A, 3B, 3C). Both FORCLIM and ZELIG also produced this pattern. Over-

all, the FORCLIM size-class frequencies fit the actual distributions somewhat better than the ZELIG frequencies do. ZELIG overestimated the density of large stems (>90 cm DBH) at the 500 m sites and the density of small stems (0–10 cm DBH) at the 1000 m sites while none of the size classes simulated by FORCLIM were similarly inaccurate (Figs. 3A, 3B, 3C).

The results above were based on a species pool of 18 species. However, only eight species were tested in previous work with ZELIG. When only these eight species, which include the dominants at most sites, were used with ZELIG and FORCLIM (Fig. 2), the major compositional trends noted above did not change. Although certain minor species were absent, the dominant species showed similar trends regardless of the size of the species pool used as model input.

Geographic Transect Gradient

When these same models were applied along broader gradients extending beyond the west slope of the Cascade Range, projected composition and total basal area diverged sharply from each other. Along the geographic transect at 44.13° N latitude (Fig. 1B), FORCLIM (with 18 species) was better able to capture several measured aspects of forest composition and basal area (Figs. 4A, 4B) than was ZELIG (with 8 species) (Fig. 4C). ZELIG was particularly inaccurate at the eastern, dry end of the gradient which should have low total basal area and, at the easternmost point of the gradient (-121° W), no forest at all (Fig. 4A). Instead, ZELIG projected *Pseudotsuga*—*Tsuga heterophylla* forests with high basal area at these sites, essentially the same as it projected at the western Cascades mid-elevation sites, a clearly unacceptable result. This result was obtained even when soil depth was reduced from 1 to 0.1 m, on the supposition that the soil moisture calculation with deep soils was not affecting tree growth.

By contrast, FORCLIM projected a low total basal area near the eastern end of the gradient, and a lack of trees at the eastern most point (Fig. 4B). Note that the CoC values (Table 1B) suggest that ZELIG has its greatest accuracy in the *Abies amabilis* and subalpine zones of the western Cascades. CoC values also demonstrate that ZELIG accuracy declines greatly both to the east and the west of the western Cascades sites. In contrast, CoC values for FORCLIM are uniformly high, if somewhat variable, along the length of the transect.

In contrast to its projection of dense forest in the non-forested eastern site, ZELIG simulates no forest at the highest-elevation site along the gradient (Fig. 4C). There, both forest survey data (Fig. 4A) and FORCLIM output describe a *Tsuga mertensiana* forest at this site (Fig. 4B). We note this difference is not necessarily important because both models could be correct at the highest elevations, where both treeless alpine areas and subalpine forests with *Tsuga mertensiana* occur.

Forested Ecoregions

FORCLIM reproduced the major vegetation patterns and total basal area trends in the series of ecoregions from wet maritime to dry continental climate (Figs. 5A, 5B). However, in some cases, FORCLIM overrepresented species that are rare or absent on the actual landscape of an ecoregion. For example, *Abies grandis* and *Pinus ponderosa* were projected to be minor species in several coastal and wet montane ecoregions where they were rare or absent. It also overestimated the amount of *Pseudotsuga* in the dry continental ecoregions (9d & 9e).

In the Western Cascades Montane Highlands ecoregion (4b), selected for simulation by ZELIG as well as FORCLIM, both models projected dominance of *Pseudotsuga* as observed in the actual field data from within the ecoregion (mean values from 10 sites; Fig. 6). However, the abundance of other species varied. The actual data showed abundant *Tsuga heterophylla*, *Abies amabilis* and *A. procera* in the ecoregion, in that order. FORCLIM projected the same species in reverse order, as other important species. By contrast, ZELIG projected *Tsuga mertensiana*, *Abies amabilis*, and *Tsuga heterophylla* as other important species. The high abundance of *Tsuga mertensiana* and the absence of *Abies procera* in the ZELIG simulations are noteworthy deviations from the actual data. The CoC values (Table 1C) indicate that FORCLIM simulations are somewhat more accurate estimators of actual vegetation in ecoregion 4b than are ZELIG simulations, although both model results may be acceptable for many applications.

Conclusions

Both models performed reasonably well in the western Cascade Range of Oregon. Simulated composition of H. J. Andrews forests at low to mid elevations, dominated by *Pseudotsuga* and *Tsuga heterophylla*, generally agreed with actual data. ZELIG did somewhat better than FORCLIM in western Cascades and eastern Coast Range forest sites dominated by *Pseudotsuga menziesii*, *Tsuga heterophylla*, and *Thuja plicata* and on this basis, ZELIG may be the better choice for applications in these forests, particularly if the applications do not involve transient shifts in moisture availability. Differences between actual composition and that simulated by both ZELIG and FORCLIM were evident in forests at higher elevations (ca. 1400 m) of the western Cascades. Under the high-elevation climate, at least one of the several actual dominant species was absent from output by both models. Although FORCLIM matched vegetation survey data better at these high elevations along the geographic transect, it is not certain that ZELIG was incorrect in simulating no trees at all (i.e., and alpine vegetation). Along broader climatic gradients in the western Oregon region, FORCLIM captured considerably more of the compositional variation than ZELIG did. FORCLIM also simulated the drought-regulated forest-steppe boundary accurately, while

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ZELIG projected dense *Pseudotsuga* forests on steppe lands where trees do not currently grow.

The major finding from this comparison of model output with actual vegetation data is that just one set of species parameters permits one to simulate much of the forest compositional response to climatic gradients in western Oregon with FORCLIM. The FORCLIM model mimicked the general compositional differences across those gradients, although some discrepancies were noted for certain sites and ecoregions. FORCLIM also captured the stand biomass trends, although simulated levels of biomass and basal area exceeded those measured at some of the sites and ecoregions examined. The ability of FORCLIM to produce reasonable trends in composition and basal area across major gradients leads us to suggest that FORCLIM is probably able to capture the variation in forest composition and structure that is generated locally by climate differences in complex terrain (i.e., slope, exposure, mountain-valley winds, and so on), and to respond with the correct species composition to chronic changes in climate. We note however, that none of the tests we applied assessed the rates at which simulated vegetation would change in response to projected rapid climate change.

Although ZELIG was superior to FORCLIM in the Cascades and Coast Range *Pseudotsuga menziesii* - *Tsuga heterophylla* forests, and although it has some very desirable capabilities (e.g., multiple interacting plots [Urban 1993], available links to the TREGRO carbon allocation model, and scaling of ozone effects [Laurence et al., 2001]), it is not as accurately applied across environmental gradients. This is a considerable disadvantage for ZELIG within the complex terrain of western Oregon. A single set of species parameters does not produce the variation in composition observed along broad climatic gradients in western Oregon. Thus, it appears that ZELIG requires species re-parameterization when moved from one site to another with differing climate. This limitation casts doubt on the suitability of ZELIG for assessments of forest response to climatic changes that are great enough to force shifts in forest composition, or from forest to steppe. It also suggests that regional analyses of forest response to changing atmospheric chemistry (i.e., ozone shifts) with ZELIG require, at the least, multiple parameterizations of the model.

Acknowledgements

We are very grateful to Steve Garman, Oregon State University, for generously providing the computer code for his PNWGAP 1.0 version of the ZELIG model, and for his useful advice during our work on this project. We are grateful to Connie Burdick, Western Ecology Division, U.S. EPA, for the time and efforts she expended in providing geographic data and creating the map of CVS plot sites and ecoregions (Fig. 1A). Sarah Shafer, U.S. Geological Survey, also provided assistance with geographic data. An earlier draft of the manuscript was considerably strengthened by constructive

and helpful reviews by Steven Garman, Robert Pabst, Oregon State University, John Laurence, U.S.D.A. Forest Service, and David Tingey, U.S. Environmental Protection Agency.

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