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Calibrating and testing a gap model for simulating forest management in the Oregon Coast Range

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ABSTRACT

The complex mix of economic and ecological objectives facing today's forest managers necessitates the development of growth models with a capacity for simulating a wide range of forest conditions while producing outputs useful for economic analyses. We calibrated the gap model ZELIG to simulate stand-level forest development in the Oregon Coast Range as part of a landscape-scale assessment of different forest management strategies. Our goal was to incorporate the predictive ability of an empirical model with the flexibility of a forest succession model. We emphasized the development of commercial-aged stands of Douglas-fir, the dominant tree species in the study area and primary source of timber. In addition, we judged that the ecological approach of ZELIG would be robust to the variety of other forest conditions and practices encountered in the Coast Range, including mixed-species stands, small-scale gap formation, innovative silvicultural methods, and reserve areas where forests grow unmanaged for long periods of time. We parameterized the model to distinguish forest development among two ecoregions, three forest types and two site productivity classes using three data sources: chronosequences of forest inventory data, long-term research data, and simulations from an empirical growth-and-yield model. The calibrated model was tested with independent, long-term measurements from 11 Douglas-fir plots (6 unthinned, 5 thinned), 3 spruce-hemlock plots, and 1 red alder plot. ZELIG closely approximated developmental trajectories of basal area and large trees in the Douglas-fir plots. Differences between simulated and observed conifer basal area for these plots ranged from -2.6 to 2.4 m^2/ha; differences in the number of trees/ha >50 cm dbh ranged from -8.8 to 7.3 tph. Achieving these results required the use of a diameter-growth multiplier, suggesting some underlying constraints on tree growth such as the temperature response function. ZELIG also tended to overestimate regeneration of shade-tolerant trees and underestimate total tree density (i.e., higher rates of tree mortality). However, comparisons with the chronosequences of forest inventory data indicated that the simulated data are within the range of variability observed in the Coast Range. Further exploration and improvement of ZELIG is warranted in three key areas: (1) modeling rapid rates of conifer tree growth without the need for a diameter-growth multiplier; (2) understanding and remedying rates of tree mortality that were higher than those observed in the independent data; and (3) improving the tree regeneration module to account for competition with understory vegetation.

1. Introduction

As forest management changes to meet a new mix of ecological and commodity objectives, forest growth and succession models must change as well. Empirical forest growth-and-yield models typically are not developed to deal with novel silvicultural approaches (e.g., green tree retention, mixed-species stands, or long rotations) or to predict non-commodity aspects of forest structure such as understory development or deadwood dynamics. Gap models, on the other hand, are based on successional processes, can simulate a wider variety of stand structures, and can make projections over longer time periods.

There is ongoing debate on the practicality and reliability of using gap models to address forest management questions (e.g.,

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Monserud, 2003). Gap models have produced reasonable estimates of tree diameter distributions and dominance-diversity (Doyle, 1981), basal area, leaf area index and tree height (Leemans and Prentice, 1987), as well as biomass and net primary productivity (Jiang et al., 1999). In contrast, the shortcomings of gap models have prompted modifications and recommendations for improving them. For instance, Lindner et al. (1997) better estimated tree mortality by incorporating measures of competition into a gap model's height-growth function, which in most gap models is independent of stand density. Changing the tree regeneration function in gap models has been recommended to account for seed production, seed dispersal, seedling establishment, canopy shading and herbivory (Price et al., 2001; Wehrli et al., 2007). Others (see reviews in Schenk, 1996; Hinckley et al., 1996; Loehle and LeBlanc, 1996; Monserud, 2003) point to the limitations of the parabolic temperature response function used in some gap models, arguing that an asymptotic function, which does not restrict tree growth with increasingly warmer temperatures, better reflects the ability of tree species to grow outside their current geographic ranges. There is also the question of whether gap models developed for one geographic or climatic region can be transferred to another, given the potential for different drivers of forest growth (Bugmann et al., 1996) and the need for local or regional data to parameterize a model (Robinson and Monserud, 2003). Despite these shortcomings, gap models continue to be used and improved upon in a broad array of applications in forestry, including large-scale assessments of forest policies across multiple land ownerships.

Understanding the cumulative effects of forest management across ownerships is central to evaluating forest policies and developing sustainable forest management systems. Few forest ecological studies, however, have addressed this issue and worked at this scale. The Coastal Landscape Analysis and Modeling Study (CLAMS) (Spies et al., 2007a) assessed how different forest policies, practices and land uses might affect ecological attributes (such as the amount of late-successional forest or the distribution of wildlife habitat) and socioeconomic indicators (such as timber harvest volumes and recreation values) for 100 years across ownerships in the Oregon Coast Range. A fundamental building block of this landscape-scale analysis was the simulation of stand-level dynamics, which was accomplished using a modified version of the gap model ZELIG (Urban, 1990). We selected ZELIG for CLAMS because we expected it to be robust to the variety of forest conditions and practices encountered in the Coast Range, including mixed-species stands, small-scale gap formation, innovative silvicultural methods, intensively grown plantations, and reserve areas where forests grow unmanaged for long periods of time.

ZELIG was modified for the Pacific Northwest (Garman et al., 1992; Urban, 1993) from the original version (Urban, 1990), which traces its origins to JABOWA (Botkin et al., 1972) and FORET (Shugart and West, 1977). Among the modifications to ZELIG.PNW was a forest management "event scheduler" to simulate silvicultural activities (Garman et al., 1992), allowing exploration of management effects on stand structure (Garman et al., 2003), wildlife habitat (Hansen et al., 1995) and wood production (Busing and Garman, 2002). ZELIG.PNW was parameterized for the western hemlock *(Tsuga heterophylla)* vegetation zone (Franklin and Dyrness, 1973) using data from the Cascade Mountains of Oregon (Garman et al., 1992; Hansen et al., 1995). And although much of the CLAMS study area (Oregon Coast Range) is in the western hemlock zone, it is distinguished from the Cascades by its climate, soils, tree-species distributions, forest productivity, and disturbance regimes. Therefore, it was necessary to parameterize ZELIG.PNW (hereafter "ZELIG") specifically for the Coast Range.

We had multiple objectives in calibrating ZELIG for CLAMS. First, we needed reasonable estimates of stand growth across a diversity of forest types because the stand-level simulations were scaled up for landscape-level analyses (Spies et al., 2007a). Second, we needed to accurately simulate densities of large trees and other structural attributes that were used as inputs in our models of wildlife habitat (Spies et al., 2007b). Third, we needed to simulate a range of silvicultural practices and management objectives, with particular attention to young Douglas-fir forests managed intensively for wood fiber. Fourth, we needed ZELIG to generate reliable estimates of timber volumes which influenced harvest scheduling in our landscape simulator (Johnson et al., 2007). In this paper we report on our efforts to calibrate ZELIG for the Oregon Coast Range and evaluate the model's performance against independent, long-term data on forest development. Our approach to calibrating model parameters was unique in that it was based on both observational data from permanent plots and simulated data from a growth-and-yield model. Furthermore, this is one of only a handful of studies (e.g., Lindner et al., 1997; Yaussy, 2000; Larocque et al., 2006) to utilize long-term independent data for testing a gap model's performance, and the first we know of to test a gap model with long-term data from thinned stands in forest types of the Pacific Northwest.

2. Methods

2.1. Methods-study area

The Coast Range physiographic province occupies 2.3 million ha in western Oregon (Fig. 1). It is characterized by rugged mountains dissected by a dense network of streams and rivers. Underlying geology is primarily uplifted ocean sediment (sandstone and siltstone) with some volcanic (basalt) intrusions. Elevations range from sea level to about 1300 m, with most ridge tops ranging from 450 to 750 m. Winters have moderate temperatures and abundant rainfall, whereas summers are warm and dry. Persistent summer fog along the coast typifies the fog ecoregion (Pater et al., 1998), where Sitka spruce *(Picea sitchensis)* defines a vegetation zone distinct from the western hemlock zone (interior ecoregion). The Coast Range is recognized for its highly productive conifer forests (Waring and Franklin, 1979), with Douglas-fir *(Pseudotsuga menziesii)* as the dominant tree species. Other major tree species modeled in this project include western hemlock, Sitka spruce, western redcedar *(Thuja plicata)*, red alder *(Alnus rubra)* and bigleaf maple *(Acer macrophyllum)*. Forests of the Coast Range have been shaped extensively by logging and wildfires since the mid-1800s, resulting in a landscape that is a mosaic of young, even-aged conifer plantations, unmanaged mature forests, small clusters of hardwoods, and remnant patches of old growth.

2.2. Methods-model function and structure

ZELIG simulates tree growth, tree regeneration and tree mortality on an annual time step. Growth and regeneration are modeled by estimating maximum potential behavior and then constraining that behavior by limiting light, soil moisture, soil fertility, and ambient temperature. Diameter growth is a function of leaf area, canopy position relative to other trees, and tolerance to shading. Tree height is related to diameter by species-specific allometric equations, the coefficients for which can be adjusted to represent different site classes for most species (Garman et al., 1995). We further differentiated site classes (high vs. medium) with species-specific diameter-growth multipliers which fine-tuned tree growth to better match empirical observations. Site class distinctions are particularly important and relevant in

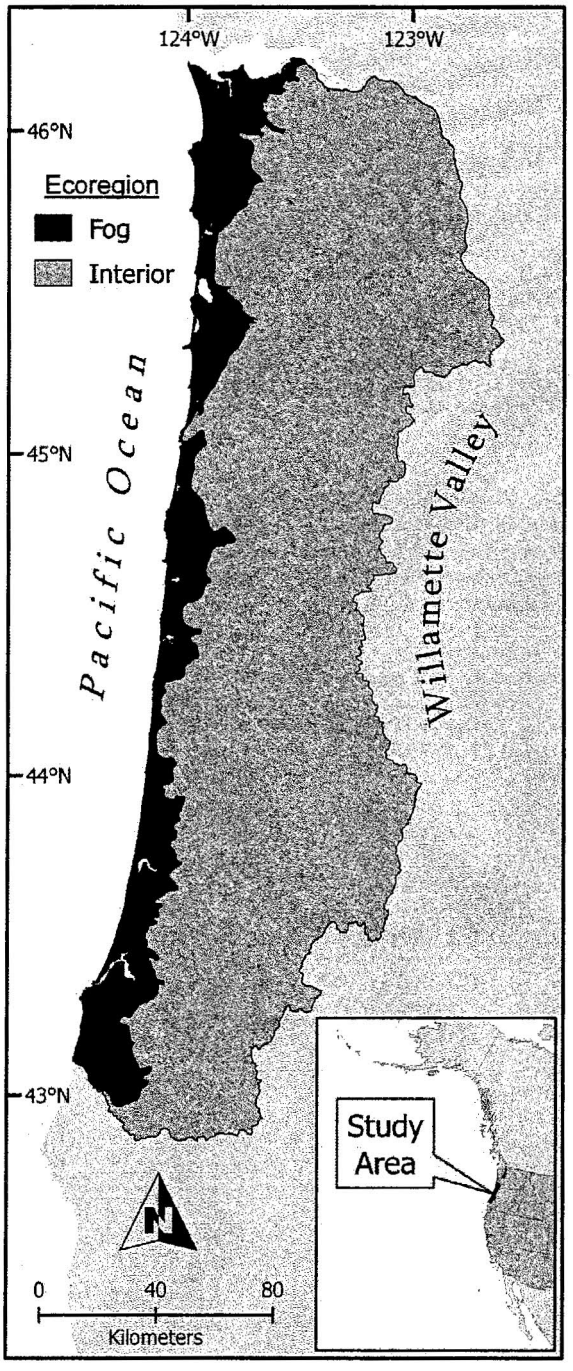

Fig. 1. Study area and ecoregions (adapted from Pater et al., 1998) for the Coastal Landscape Analysis and Modeling Study.

even-aged stands such as the forest plantations that are common in our study area. At 50 years on high sites (classes 1-2), Douglas-fir are >35 m tall, and on medium sites (classes 3-5) they are 15-35 m tall (King, 1966). Annual cubic volume production in ZELIG is related to species-specific growth efficiency (volume growth per unit leaf area) (Waring, 1983; Waring and Schlesinger, 1985; Urban et al., 1993). The potential for regeneration to occur for any given species is determined by (1) its regeneration ranking, essentially a proxy for its abundance in the stand and surrounding landscape relative to other species; and (2) a probability governing the likelihood of establishment given its ecological requirements and response to competition. The modeling of tree mortality includes both density-dependent (competition/suppression) and density-independent ("ambient") mortality. The probability of density-dependent mortality in any given year increases when a tree's growth rate is less than 10% of its optimum or absolute diameter growth is less than 0.1 mm in the preceding three years. The probability of ambient mortality is a function of the maximum longevity for each species, and is applied equally at each time step to all stems of a species regardless of the stem's growth rate, size or competitive environment. Ambient mortality emulates tree death that might result from factors such as localized windthrow, disease or insect attacks.

ZELIG simulates the forest as a collection of gaps. Each gap represents the area potentially occupied by a canopy dominant tree (Urban and Shugart, 1992), which in our model is 20 m x 20 m, or 0.04 ha, We used a 5 x 5 grid of 25 gaps for a total simulation area of 1 ha. ZELIG simulates each gap through time, tracking diameter, height, and live crown of individual trees. Leaf area is tracked in 1-m increments along individual tree boles, allowing the model to track tree-level crown recession as a function of a species' shade tolerance. Light penetration through tree canopies takes into account the vertical leaf-area profiles among neighboring gaps (grid cells). To model light penetration in cells on the perimeter of the grid, ZELIG "wraps" the grid cells in question to the opposite side, creating a continuous simulation area and mitigating edge effects.

2.3. Methods-modifying environmental and species parameters

We tailored ZELIG for the Coast Range by modifying environmental and species parameters. The modified environmental parameters were latitude, longitude, mean elevation, mean monthly temperature and precipitation, and monthly solar radiation. We used separate environmental driver files to distinguish the fog and interior ecoregions. Monthly temperature and precipitation values were extracted from PRISM (Parameter-elevation Regressions on Independent Slopes Model) (Daly et al., 1997) for a representative location in each ecoregion.

Species parameters were also modified, including annual degree-day limits, growth efficiency, and rankings for shade tolerance and tree regeneration (Table 1). Maximum age was adjusted slightly for some species based on tree-core data from the Coast Range (Poage, 1994) and the literature. Species range maps (Little, 1971) were used to determine the southern- and northern-most occurrence of each species, from which degree-day limits were determined using PRISM for locations within the continental U.S. and weather-station data for locations in Alaska (WRCC, 1999) and British Columbia (CMC, 1999). Results of some of the initial comparisons with calibration data indicated that species interactions were over-sensitive to temperature - a finding consistent with that of Fischlin et al. (1995) - so we broadened the temperature limits of each species by 200 degree-days at both the upper and lower ends. The expanded number of degree-days was chosen subjectively but is supported by evidence (Bonan and Sirois, 1992; review by Loehle and LeBlanc, 1996) that tree species have the capacity to grow both north and south of their current geographic ranges. Tree regeneration probabilities were modified for the purpose of distinguishing potential successional pathways. There were six sets of probabilities (pathways), each with species-specific values. Probabilities varied by ecoregion, initial stand cover type (hardwood vs. conifer or mixed), and the presence and crown class of shade-tolerant conifers (a potential seed source) in the initial tree list. The probabilities for a given plot were fixed throughout the simulation.

Table 1
Species parameters[a] used in ZELIG simulations of conifer stands in the interior ecoregion of the Coast Range

Species[b]	A_{max}	M_A	D_{max}	G	LF	GDD (min-max)	S_{tol}	D_{tol}	N_{tol}	Reg[c]	SP	D_H	D_M
Acma	300	0.015	250	2976	6	872–4141	2	20	2	2	1	1.0	1.0
Alru	140	0.033	150	2380	9	604–3354	4	20	0	5	1	1.0	1.0
Pisi	800	0.006	400	2600	5	450–2494	2	10	2	0	0	1.3	1.1
Psme	1100	0.004	300	2520	3	906–3680	4	40	2	5	0	1.5	1.2
Thpl	1500	0.003	300	1963	10	823–3111	1	30	2	2	0	1.0	1.0
Tshe	700	0.007	225	1400	4	450–2785	1	30	2	3	0	1.3	1.1

Species parameters for stands dominated by broadleaved hardwoods or stands in the fog ecoregion were the same except for regeneration ranking.

[a] A_{max}: maximum age attained by species (years); M_A: ambient annual mortality rate = $-\ln(.01)/A_{max}$; D_{max}: maximum dbh attained by species (cm); G: growth efficiency (cm^3 of wood/m^2 leaf area); LF: leaf form; GDD: growing degrees-days; minimum and maximum correspond to each species' northern and southern range limits which were then extended by 200 degrees in each direction; S_{tol}: shade tolerance ranking; D_{tol}: drought tolerance ranking; N_{tol}: soil nutrient tolerance ranking; Reg: tree regeneration ranking; SP: sprouting potential indicator; D_H: diameter-growth multiplier for high site classes; D_M: diameter-growth multiplier for medium site classes.

[b] Acma = bigleaf maple; Alru = red alder; Pisi = Sitka spruce; Psme = Douglas-fir; Thpl = western redcedar; Tshe = western hemlock.

[c] Different regeneration rankings were used for some species in the fog ecoregion and in hardwood stands, as follows: Pisi: 4 in fog-zone conifer stands, 1 in all hardwood stands; Psme: 3 in fog-zone conifer stands, 1 in all hardwood stands; Thpl and Tshe: 1 in all hardwood stands.

2.4. Methods-calibrating ZELIG

Calibrating ZELIG for the Oregon Coast Range was based on comparisons with three complementary data sources: (1) chronosequences of stand attributes constructed from forest inventory data, (2) long-term plot data from Cascade Head Experimental Forest in the fog ecoregion, and (3) simulations from ORGANON (Hann et al., 1997), an empirical growth-and-yield model used widely in the Pacific Northwest. In the initial stages of calibration, all parameter modifications in ZELIG were reassessed with each of

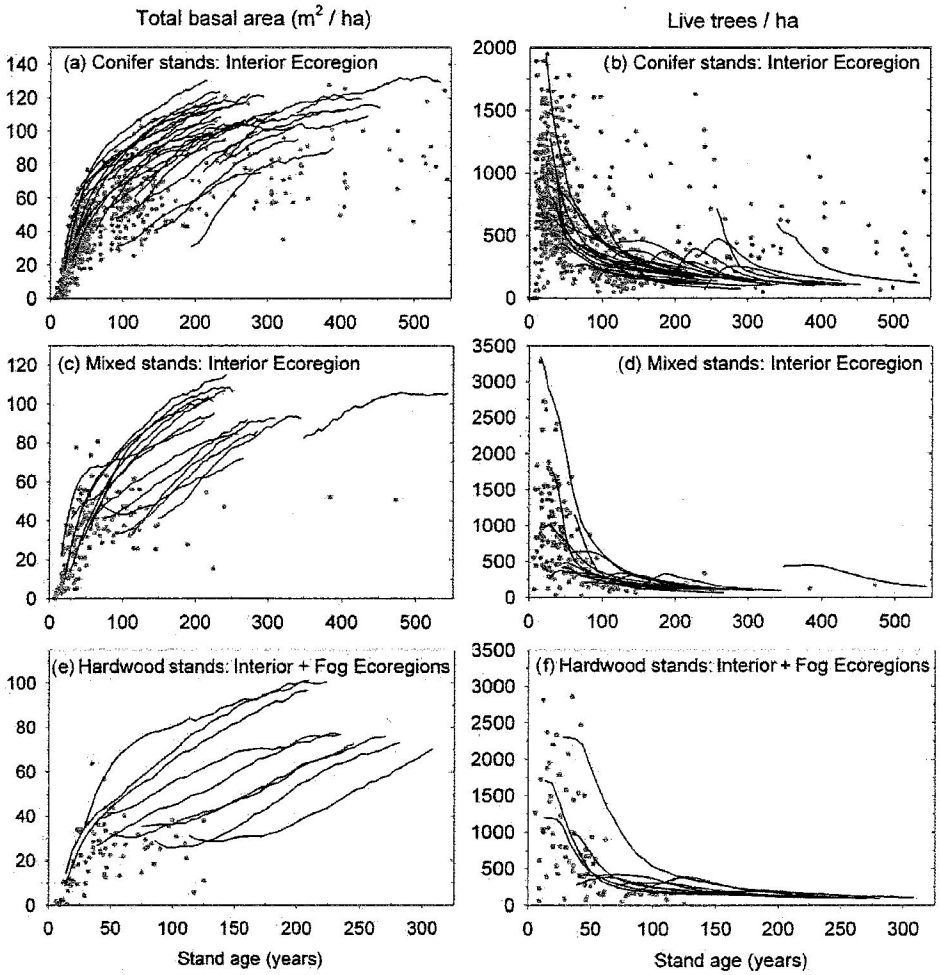

Fig. 2. (a–f) Inventory data for chronosequences (gray circles) of total basal area and live-tree density from (a and b) conifer-dominated stands in the interior ecoregion, (c and d) mixed conifer-hardwood stands in the interior ecoregion, and (e and f) hardwood-dominated stands from the interior and fog ecoregions of the Oregon Coast Range. A subset of the chronosequence plots was simulated in ZELIG (black lines) to examine model performance relative to the chronosequences. Simulations shown were run with the final model settings.

Table 2
Characteristics of independent data sets from Black Rock State Forest (BR) and Cascade Head Experimental Forest (CH) used for testing ZELIG

Plot ID	Dominant species[a]	Site index[b]	Site Class	Plot area (ha)	Initial conditions			Treatment	Data record length (years)	Number of data points
					Age (years)	Basal area (m^2/ha)	Density (trees/ha)			
BR-7	Psme	43	High	0.4	39	45.1	1228	Not thinned	41	27
BR-9	Psme	N/A	N/A	0.4	39	40.4	1722	Not thinned	50	20
BR-12	Psme	42	High	0.4	46	47.7	805	Not thinned	38	25
BR-19	Psme	33	Med	0.4	49	50.4	1003	Not thinned	37	19
BR-27	Psme	34	Med	0.4	47	48.8	1200	Not thinned	40	16
BR-1	Psme	38	High	0.4	39	35.5[c]	921	5 thinnings	41	30
BR-4	Psme	41	High	0.4	40	30.8[c]	941	5 thinnings	41	29
BR-25	Psme	38	High	0.4	49	47.4	793	4 thinnings	47	15
BR-30	Psme	32	Med	0.4	46	39.4[c]	929	4 thinnings	40	15
BR-35	Psme	N/A	N/A	0.4	44	57.7	877	3 thinnings	36	14
CH-4	Pisi/Tshe	30*	Med	0.4	85	99.1	474	Unmanaged	44	6
CH-7	Tshe/Pisi	30*	Med	0.4	85	99.3	630	Unmanaged	44	6
CH-8	Tshe	30*	Med	0.4	85	100.4	884	Unmanaged	44	6
CH-23	Alru/Pisi	40	High	0.2	12	<1	3068	Unmanaged	60	9
CH-41	Psme	N/A	N/A	0.4	67	64.7	373	Unmanaged	60	10

[a] Alru = red alder; Pisi = Sitka spruce; Psme = Douglas-fir; Tshe = western hemlock.
[b] Site index is height in meters for Douglas-fir at age 50 (King, 1966) unless noted by an asterisk, in which case it is for western hemlock at age 50 (Wiley, 1978).
[c] Thinned in first year of study; pre-thinning data not available.

the three data sources. Once the model was performing acceptably, we further refined ZELIG through additional comparisons with ORGANON and then checked the effect of the final changes by reevaluating comparisons between ZELIG and the chronosequence data. By calibrating ZELIG to these different data sources, we sought to incorporate the predictive ability of an established empirical model with the flexibility of a forest succession model.

The chronosequence data were used to represent successional development of three stand types (conifer, hardwood, mixed conifer-hardwood) in each of the two ecoregions, allowing us to assess whether trends simulated by ZELIG were consistent with data from across the forested landscape. The chronosequence concept assumes that a developmental trajectory represented by different stand locations and ages is a suitable replacement for change over time. The number of data points in each chronosequence ranged from as few as 13 for hardwood stands to 732 for conifer stands in the interior ecoregion. Stand ages ranged from 0 to nearly 500 years; the relative lack of data points in the mixed and hardwood stand types beyond 150 years reflects natural succession to conifer dominance. We simulated a subset of the inventory plots in each chronosequence to examine whether ZELIG-modeled trajectories of various attributes fell within the cloud of points in the chronosequence. These simulations were repeated following the other calibration steps (Fig. 2a-f). We examined total and species-specific basal area, quadratic mean diameter (QMD), the density and size diversity of certain dbh classes (e.g., trees>100 cm dbh) and species groups (e.g., shade-tolerant conifers). On the basis of these comparisons and other information (Harcombe, 1986; Greene et al., 1992; Pabst and Spies, unpublished data), we modified growth efficiency values, regeneration rates and ambient mortality rates for several species.

The plots from Cascade Head (Berntsen, 1961; Harcombe et al., 1990; Acker et al., 1998a,b) provided a 50-60 year record of forest dynamics for a variety of stand types including Sitka spruce/western hemlock, Douglas-fir/hemlock, red alder/mixed conifers, and pure red alder. With these data we could examine how ZELIG modeled species interactions and the growth and mortality of species other than Douglas-fir. ZELIG was initialized with data from the first measurement, and simulations of these data were qualitatively compared with the actual stand records over time, using graphs of dbh distributions and trajectories of basal area, density and QMD of each species. Growth and regeneration parameters for western hemlock, Sitka spruce, western redcedar and red alder were adjusted as a result of these comparisons.

We used ORGANON simulations to calibrate ZELIG parameters for Douglas-fir growth. ORGANON (SMC version) was developed primarily with data from even-aged Douglas-fir stands between 20 and 80 years of age. We considered it to be an accurate simulator of these stand types, given that (a) the equations were derived from tree measurements on more than 3300 research plots from northwest Oregon to southwest British Columbia (Hann et al., 2003), and (b) the ORGANON model has undergone testing since (Hann et al., 2006). We compared the two models on a stand-by-stand basis and with stand averages using 100-year simulations of inventory data from 24 even-aged stands that were 5-35 years old at time 0 and dominated by Douglas-fir (>90% of basal area) at a wide range of initial densities (375-1025 trees/hal. We initialized both models with identical tree lists, including measured crown ratios and tree heights determined from asymptotic height-to-diameter equations (Garman et al., 1995). ZELIG's regeneration function was turned off to facilitate the comparisons with ORGANON, which does not model natural regeneration. We qualitatively compared simulated trajectories for basal area, total tree density, large-tree density, QMD, tree-size diversity and tree mortality. Comparisons showed that ZELIG lagged ORGANON in both conifer basal area and density of large trees, so we increased growth efficiency values by about 10%.

In the final step of calibration, we compared the yield of wood volume (net total board feet) in ZELIG and ORGANON using data from three young Douglas-fir plantations that represented different management intensities. Intensities varied by the extent to which competing vegetation was controlled and the type of planting stock used. Simulations of the most intensively managed stand - reflecting current-day plantation management across a substantial portion of the study area - indicated that ZELIG still lagged ORGANON in the development of large trees, and therefore volume. We used species-specific diameter-growth multipliers in ZELIG (Table 1) to achieve better correspondence with ORGANON, rather than modify the diameter-growth equation itself. Such "scaling factors" have been used elsewhere for parameterizing growth models for new areas or populations as described by Vanclay (1995).

By emphasizing correspondence with ORGANON in the last step of calibration, we risked biasing ZELIG's performance with stand types other than even-aged Douglas-fir and with attributes other

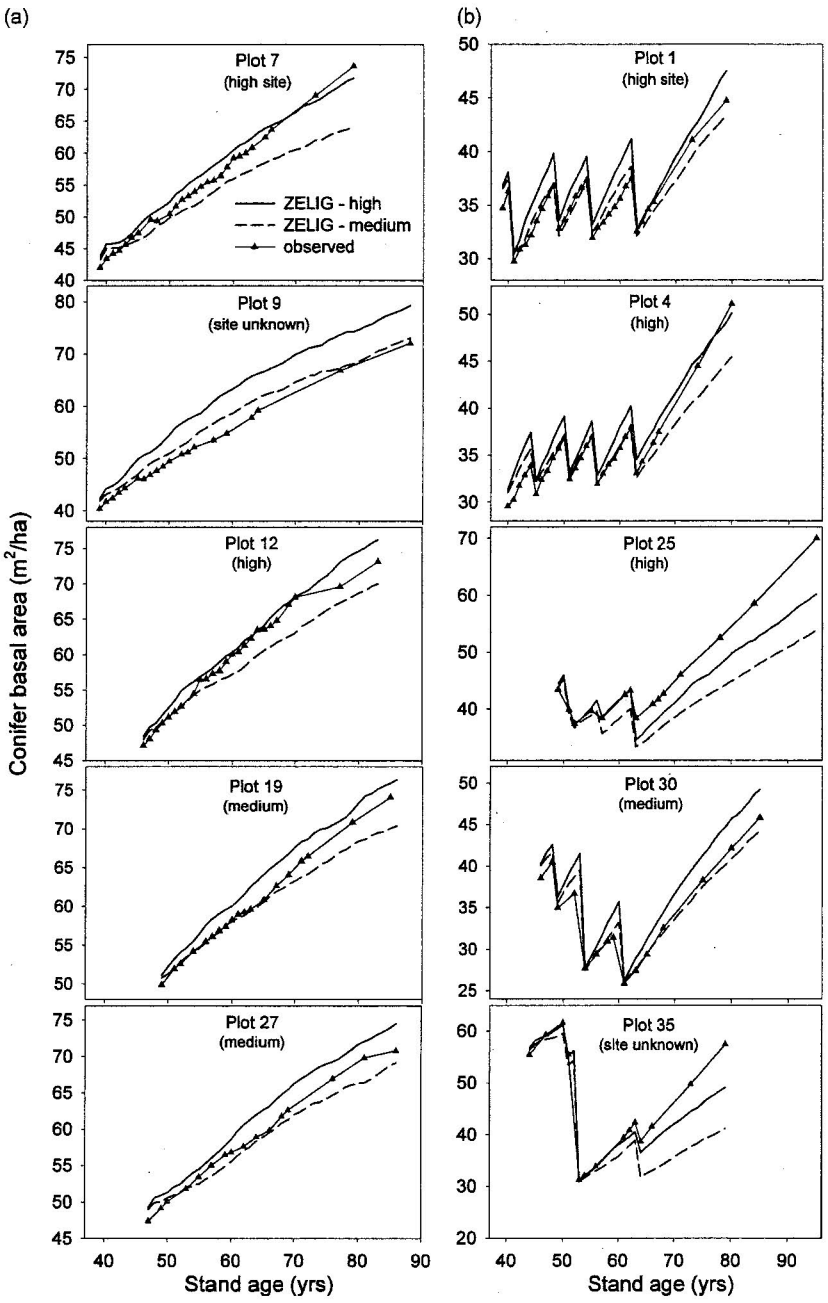

Fig. 3. (a and b) ZELIG simulations of conifer basal area over time compared with observed data from (a) unthinned and (b) thinned plots at Black Rock State Forest.

than large trees and *volume*. Therefore, we re-ran the simulations of the chronosequence plots using the final set of model parameters. The new trajectories (Fig. 2a-f) were similar to previous trajectories (not shown), and were generally within the range of variability represented by the chronosequences. Therefore, no further parameter adjustments were made. Comparisons with independent test data provided an additional mechanism for evaluating the final model.

2.5. Methods-testing ZELIG

Two sources of independent data were used to evaluate the calibrated version of ZELIG. For the interior ecoregion, we used growth-and-yield data from permanent plots at Black Rock State Forest in the east-central Coast Range. The 0.4 ha plots at Black Rock are part of an ongoing Douglas-fir thinning trial initiated in the 1950s when the naturally established trees were 39-49 years old (Curtis, 1995). Douglas-fir site indices at 50 years at Black Rock range from 32 to 41 m (site classes 1-3). We evaluated ZELIG with data from ten plots, *five* that were thinned multiple times and *five* that were unthinned controls (Table 2). The most recent measurements of these plots provided a data record spanning 40-50 years of stand growth.

We also used independent data from *five* plots at Cascade Head (Table 2) to examine how ZELIG performed for the fog ecoregion. These plots provided a growth record spanning 59-64 years. Three

Table 3
Differences between ZELIG-simulated and observed independent data from research plots at Black Rock State Forest (BR) and Cascade Head Experimental Forest (CH) in the Oregon Coast Range

Stand	Plot	Site[a]	Trmt[b]	Var[c]	Difference (ZELIG – observed)			% Relative difference		
					N[d]	Mean	Std Dev	N	Mean	Std Dev
BR	7	H	N	ConBA	27	1.4	0.9	27	2.7	1.7
				Tph50	27	6.7	6.5	21	16.1	16.2
				Tph	27	−83.1	36.7	27	−10.6	3.9
BR	9	M[f]	N	ConBA	20	1.8	0.8	20	3.6	1.5
				Tph50	20	5.2	9.1	8	[e]	[e]
				Tph	20	−166.0	67.7	20	−14.8	5.6
BR	12	H	N	ConBA	25	1.1	0.9	25	2.0	1.4
				Tph50	25	7.3	7.8	25	12.9	15.5
				Tph	25	−23.3	16.5	25	−4.0	3.0
BR	19	M	N	ConBA	19	−0.7	1.2	19	−1.0	1.8
				Tph50	19	−4.2	4.0	16	−25.5	26.4
				Tph	19	2.2	14.9	19	0.2	2.3
BR	27	M	N	ConBA	16	−0.8	1.2	16	−1.2	2.1
				Tph50	16	2.7	3.8	16	10.7	11.7
				Tph	16	−71.2	29.9	16	−9.2	3.9
BR	All control plots			ConBA	107	0.7	1.4	107	1.4	2.5
				Tph50	107	4.0	7.8	86	11.6	38.3
				Tph	107	−67.7	67.8	107	−7.7	6.4
BR	1	H	T	ConBA	30	1.9	1.0	30	5.4	2.8
				Tph50	30	4.1	3.6	30	17.7	18.3
				Tph	30	−13.1	11.7	30	−3.3	2.2
BR	4	H	T	ConBA	29	1.7	0.9	29	4.9	2.6
				Tph50	29	1.9	4.4	21	[e]	[e]
				Tph	29	−6.8	27.2	29	−2.7	4.4
BR	25	H	T	ConBA	15	−2.4	3.1	15	−4.8	5.5
				Tph50	15	−5.0	12.3	15	−4.9	10.5
				Tph	15	−13.0	12.2	15	−3.6	3.3
BR	30	M	T	ConBA	15	0.2	1.0	15	0.5	2.6
				Tph50	15	−4.3	5.5	15	−9.3	11.5
				Tph	15	17.0	18.5	15	4.3	4.0
BR	35	H[f]	T	ConBA	14	−1.6	2.5	14	−3.4	4.7
				Tph50	14	−8.8	9.6	14	−9.6	8.3
				Tph	14	−3.6	21.2	14	0.5	4.5
BR	All thinned plots			ConBA	103	0.5	2.4	103	1.9	5.4
				Tph50	103	−0.8	8.2	95	6.1	22.7
				Tph	103	−5.6	21.6	103	−1.6	4.5
CH	4	M	U	ConBA	10	−7.0	4.3	10	−5.8	3.4
				Tph50	10	−13.1	5.9	10	−5.7	2.4
				Tph	10	−156.5	176.1	10	−25.8	23.0
CH	7	M	U	ConBA	10	−4.0	4.3	10	−3.6	3.9
				Tph50	10	−6.6	7.8	10	−3.1	3.5
				Tph	10	−157.9	126.7	10	−26.6	18.5
CH	8	M	U	ConBA	10	−8.7	5.5	10	−8.3	5.1
				Tph50	10	−8.4	8.3	10	−5.1	4.6
				Tph	10	−373.7	330.8	10	−39.0	26.8
CH	23	H	U	TotBA	9	1.9	3.0	9	7.6	10.4
				Tph50	9	8.0	13.3	1	[e]	[e]
				Tph	9	345.1	373.0	9	28.2	24.9
CH	41	H	U	ConBA	9	2.6	2.8	9	3.0	3.2
				Tph50	9	−3.6	3.3	9	−2.0	1.8
				Tph	9	47.3	40.0	9	18.5	16.3
CH	All plots			ConBA	48	−3.8	5.6	44	−7.2	11.3
				Tph50	48	−5.0	10.6	40	15.3	121.9
				Tph	48	−69.8	335.2	48	−10.3	34.4

Difference expressed in units of the attribute and as a percentage of the observed value.
[a] Site class: H = high, M = medium.
[b] Treatment: N = not thinned, T = thinned, U = unmanaged.
[c] Variable: ConBA = conifer basal area (m^2/ha); TotBA = total basal area (m^2/ha); Tph50 = trees/ha ≥ 50 cm dbh; Tph = trees/ha.
[d] *N* is the number of measurement dates (years) in the observed data.
[e] Percent relative difference not shown when Tph50 for a substantial number of the observed values (divisor) was 0.
[f] Site class for plots 9 and 35 at Black Rock not known from the observed data; assumed from comparisons of simulated and observed data.

of the plots are part of a Sitka spruce/western hemlock growth-and-yield study started in the 1930s when the trees were about 85 years old (Smith et al., 1984). Tree height at 100 years for hemlock on these plots is about 44 meters, equivalent to site class 3 (Wiley, 1978; Smith et al., 1984). Of the other two plots at Cascade Head, one was established in a 12-year-old stand of red alder, and the other was part of a Douglas-fir growth-and-yield study. The plots at Cascade Head were 0.4 ha in area except for the alder plot which was 0.2 ha.

ZELIG simulations of the test data were initialized with the original tree lists from each plot and run for both high and medium site classes. Output was generated at one-year intervals to accommodate comparisons with the annual or varied measurement intervals used for the plots. Thinning events at Black Rock were simulated by matching species-specific densities in 10-cm dbh classes for the years in which thinning occurred, although ZELIG did not necessarily select the same trees that were actually thinned nor did it emulate any spatial patterns of thinning. The motivation for using this approach to thinning was our interest in evaluating simulated growth trajectories of low-density (and presumably fast-growing) stands, rather than test one of the silvicultural methods that ZELIG emulates (e.g., thinning proportionally by size to a target basal area). We tried the latter approach but found that the actual thinning events at Black Rock did not conform to one of the "canned" styles of simulated thinning, making growth comparisons difficult.

We evaluated ZELIG's performance with the test data in three ways: (1) plotting trajectories of observed versus simulated stand attributes (basal area, total tree density, density of large trees); (2) calculating the difference and percent relative difference between

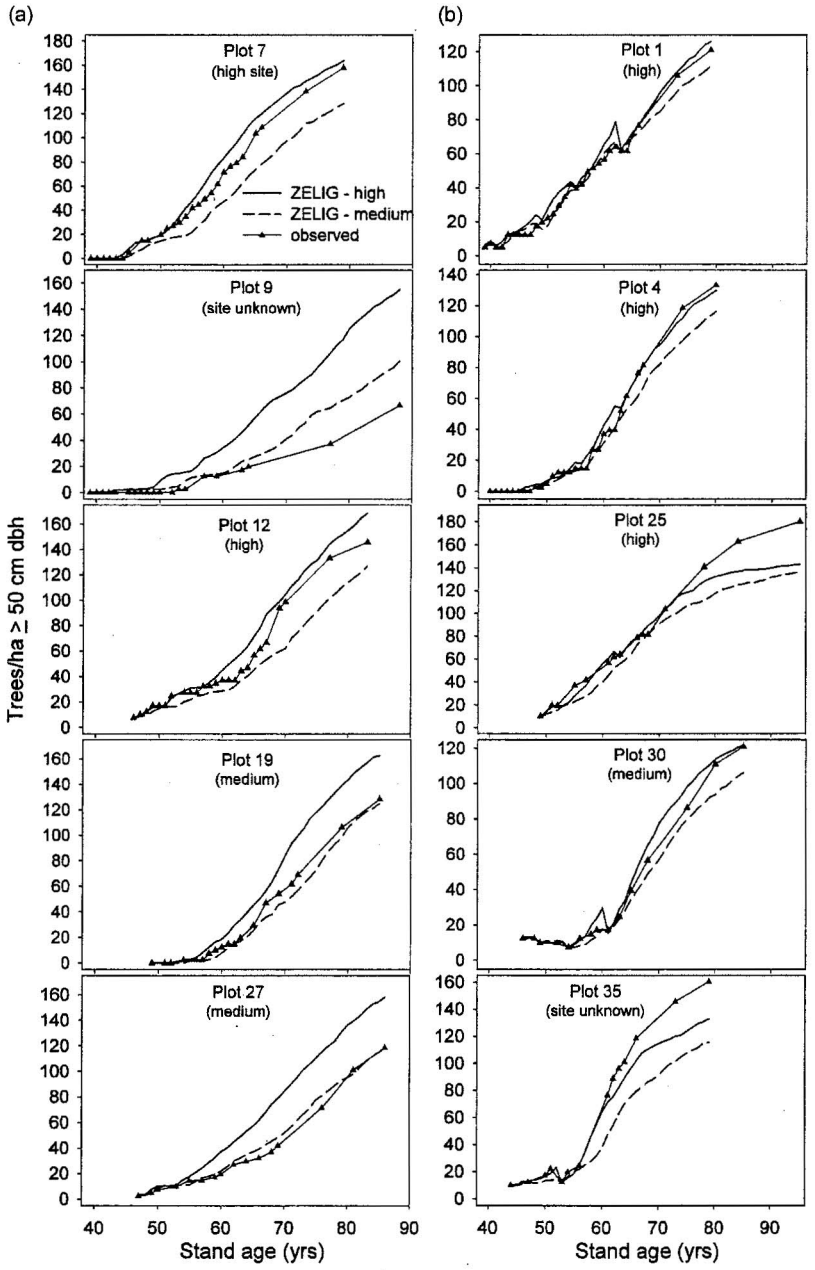

Fig. 4. (a and b) ZELIG simulations of trees/ha ≥50 cm dbh over time compared with observed data from (a) unthinned and (b) thinned plots at Black Rock State Forest.

the simulated and observed trajectories for the corresponding site class at each measurement date, with percent relative difference calculated as

$$\left[\frac{\text{Simulated value} - \text{Observed value}}{\text{Observed value}}\right] \times 100;$$

and (3) examining dbh distributions (histograms of tree density by species and dbh class) of the observed and simulated data for the most recent measurement date. Our goal in testing was to examine trends and identify potential biases in ZELIG, while recognizing that the test data represent a very small sample of the forest types we were simulating in ClAMS. We did not employ statistical tests in the comparisons, which can be inconclusive and may produce contradictory results (Yang et al., 2004).

3. Results

3.1. Testing ZELIG-Black Rock State Forest

ZELIG simulations compared favorably with observed stand development at Black Rock, particularly for the unthinned control plots (Fig. 3a). For example, the average difference between simulated and observed conifer basal area for the five unthinned plots ranged from -0.8 to +1.8 m^2/ha (Table 3), with relative difference no greater than 6% (±) for any individual measurement date. Simulated development of large trees (>50 cm dbh) in the unthinned plots also closely matched the observed data, except in plot 9 for which ZELIG overestimated large-tree density after age 59 (Fig. 4a). There was less agreement between the simulated and

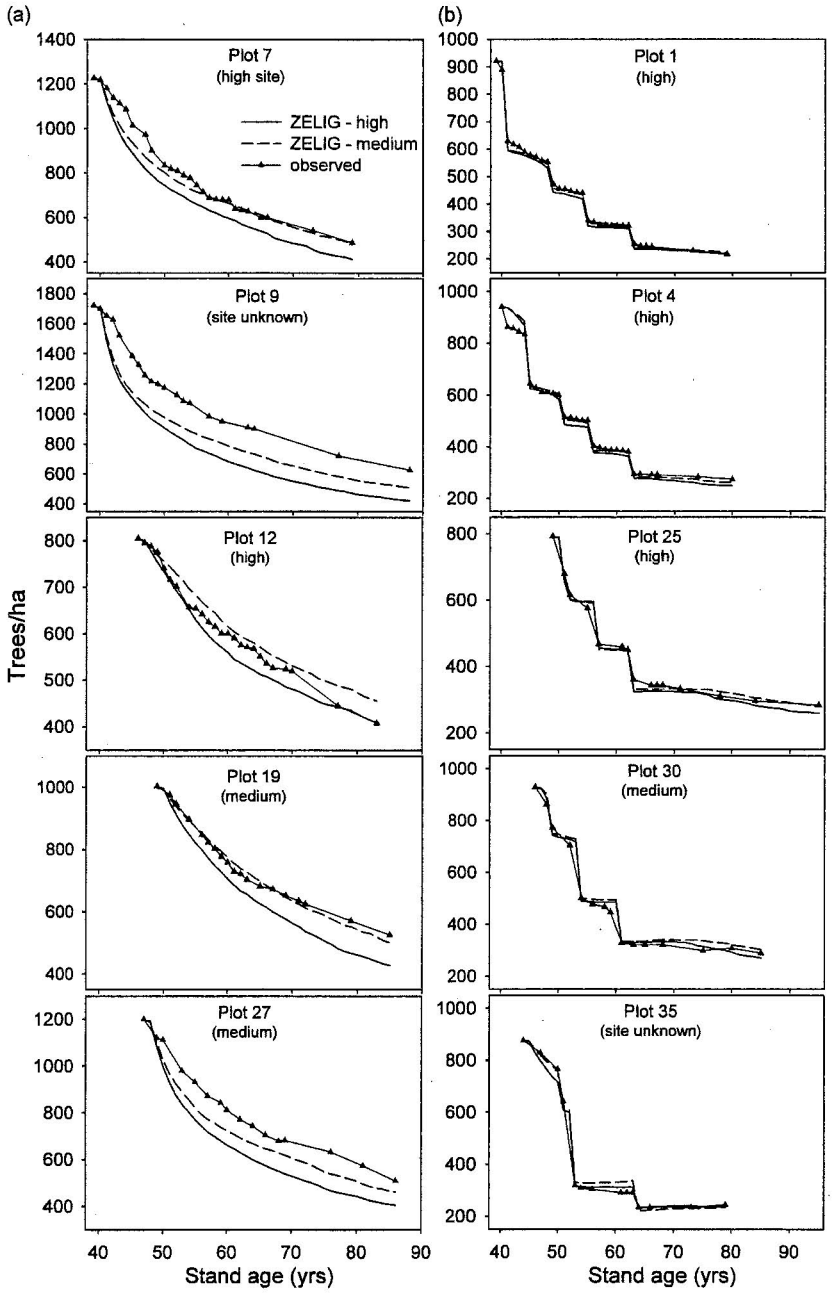

Fig. 5. (a and b) ZELIG simulations of total tree density (trees/ha) over time compared with observed data from (a) unthinned and (b) thinned plots at Black Rock State Forest.

observed data for total tree density (Fig. 5a), where deviations on the unthinned plots ran as high as 250 tph (plot 9). On a percentage basis, average relative difference in total density ranged from -14.8% to +0.2% (Table 3). Simulated dbh distributions for the most recent measurement in the unthinned plots approximated the observed distributions (Fig. 6a). However, ZELIG produced more regeneration of shade-tolerant trees, particularly in plots 7 and 12, and generally retained fewer trees in the overstory than in the observed data.

Simulations of the thinned plots at Black Rock were less accurate than those of the unthinned plots. Average differences between simulated and observed basal area, however, were still relatively small, ranging from -2.4 to 1.9 m^2/ha. The simulated trajectory of conifer basal area after the final thinning lagged appreciably in two plots (25 and 35, Fig. 3b); this difference appears to be the result of fewer trees in the upper diameter classes (Figs. 4b and 6b). The most striking difference between ZELIG and observed data is in the understory. The observed data for three of the thinned plots (1,4, 30) exhibit a bimodal distribution of tree dbh with substantial numbers of small Douglas-fir (Fig. 6b). In plots 1 and 4, all of the small Douglas-fir existed at the time of plot establishment (some 40 years earlier), and have persisted but grown little since then. In plot 30, all of the Douglas-fir and western

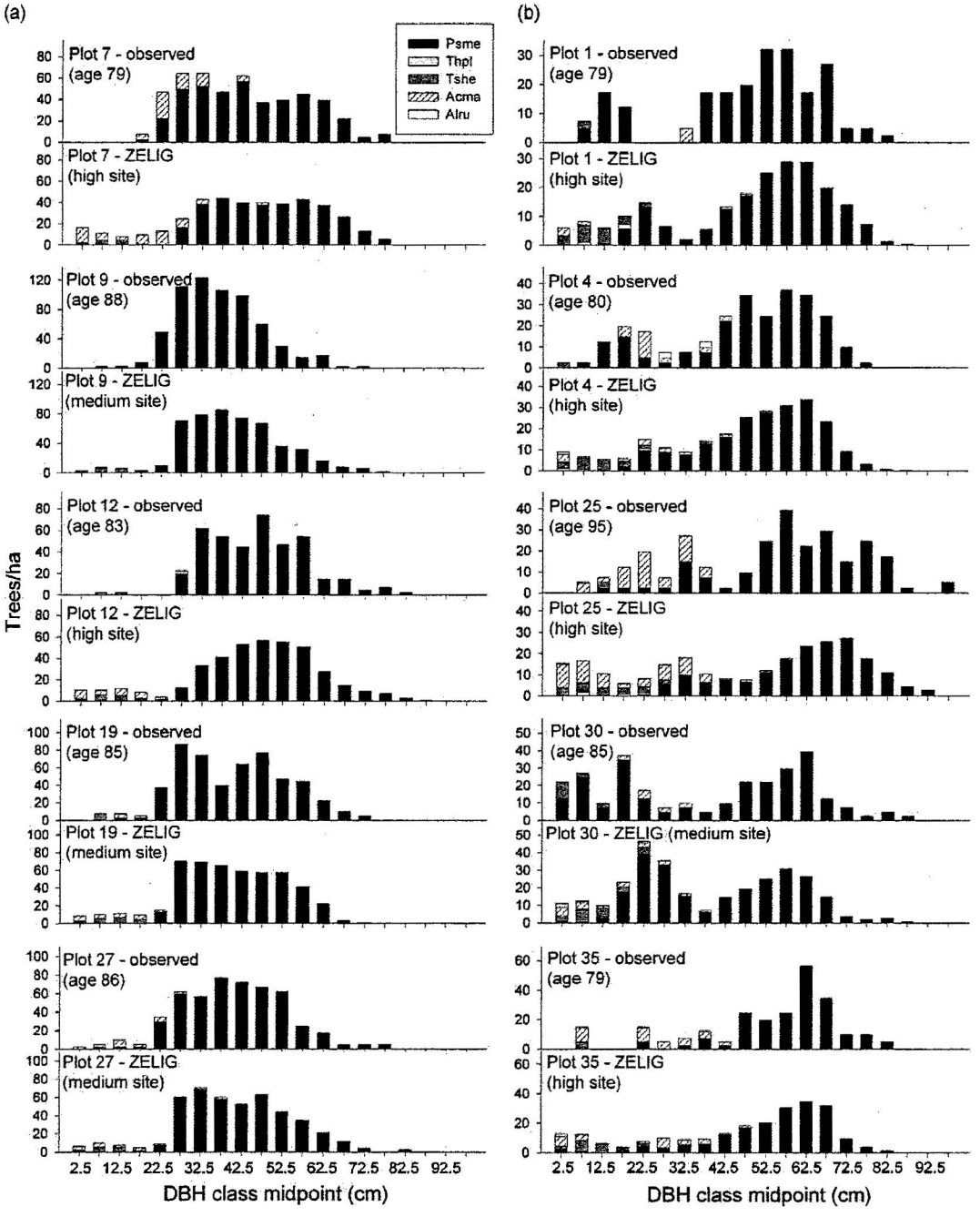

Fig. 6. (a and b) Comparison of observed and ZELIG-simulated dbh distributions for the most recent measurement of (a) unthinned and (b) thinned plots at Black Rock State Forest. Because site class could not be verified for plots 9 and 35, the simulated distributions show the site class that best matched the observed data in the trajectories from Figs. 3–5. Species abbreviations: Acma = bigleaf maple; Alru = red alder; Psme = Douglas-fir; Thpl = western redcedar; Tshe = western hemlock.

hemlock trees less than 10 cm dbh (classes 2.5 and 7.5 cm) regenerated since plot establishment. A bimodal distribution is also apparent in plot 25, with the lower tier occupied primarily by bigleaf maple trees that were present when the plot was established. ZELIG simulated a bimodal distribution of dbh in plots 1 and 30, although the smaller Douglas-fir grew into larger diameter classes than in the observed data. ZELIG did not produce the Douglas-fir regeneration seen in plot 30. In both the thinned and unthinned plots, ZELIG overpredicted the establishment of shade-tolerant hemlock and maple. It is not known if the regenerating trees at Black Rock are scattered throughout the plot as a lower canopy layer, or if they are concentrated in openings created by thinning.

3.2. Testing ZELIG-Cascade Head Experimental Forest

The correspondence of ZELIG projections with the data from Cascade Head was variable. For the plots dominated by either Sitka spruce (plot 4) or western hemlock (plots 7 and 8), conifer basal area predicted by ZELIG did not keep pace with the observed data

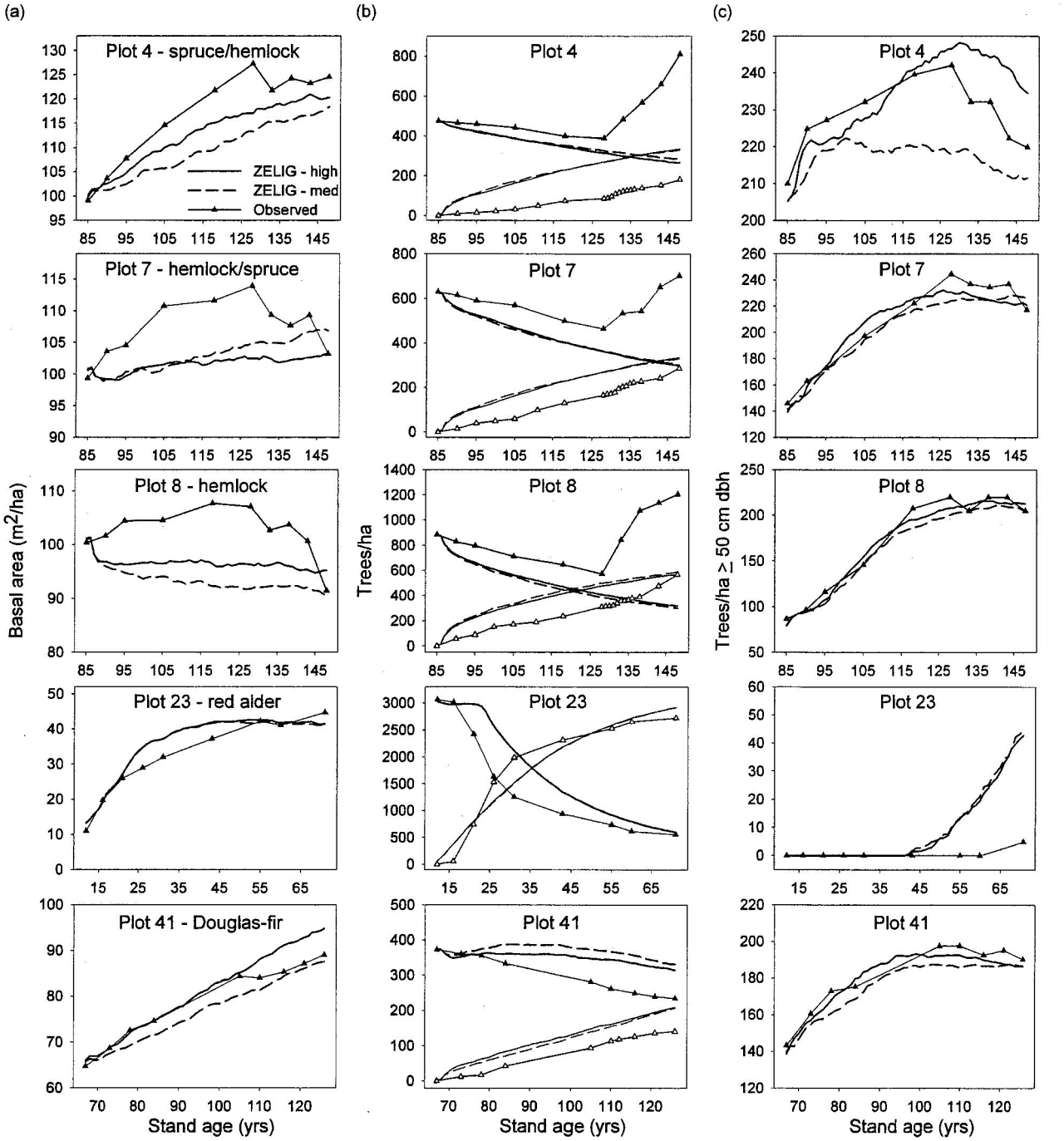

Fig. 7. (a–c) ZELIG simulations of stand attributes compared with observed data from five plots at Cascade Head Experimental Forest: (a) conifer basal area (m^2/ha) except for Plot 23 which is total basal area, (b) density (tph) of live trees and cumulative density (tph) of dead trees, and (c) trees/ha ≥50 cm dbh.

(Fig. 7a). Average percent difference for basal area ranged from −4% to −9% for these three plots (Table 3). The lag appears to be a function of higher tree mortality in ZELIG (Fig. 7b) rather than slower growth, since ZELIG tracks the development of large trees reasonably well (Fig. 7c) while differing in modeled tree densities (Fig. 7b).

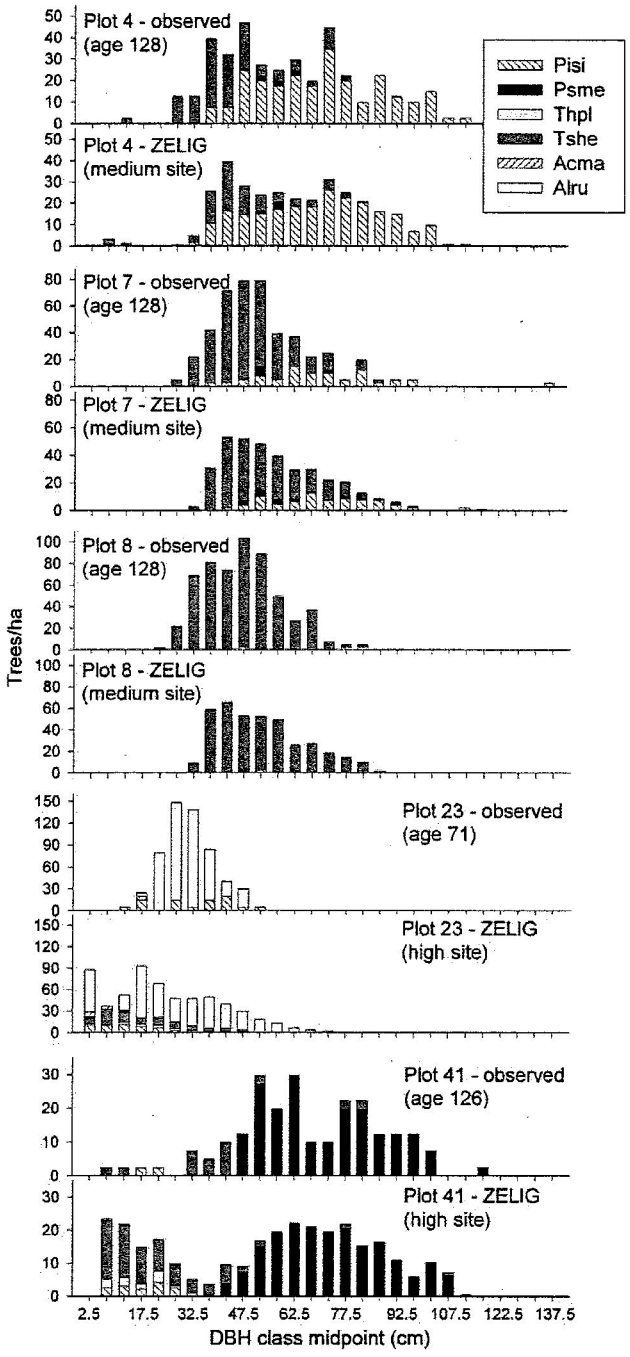

Fig. 8. Comparison of observed and ZELIG-simulated dbh distributions of five plots at Cascade Head Experimental Forest. Dbh distributions for plots 4, 7 and 8 are for the point in time preceding a major windstorm; distributions for plots 23 and 41 are for the most recent field measurement. Site class was not known for plots 23 and 41, so the simulated distributions are for the site class that best matched the observed data in the trajectories from Fig. 7. Species abbreviations: Acma = bigleaf maple; Alru = red alder; Pisi = Sitka spruce; Psme = Douglas-fir; Thpl = western redcedar; Tshe = western hemlock.

Significant windstorms in 1981 and 1983 (Harcombe, 1986; Acker et al., 2000) led to declines in observed basal area and density of large trees (Fig. 7c) on plots 4, 7 and 8 after stand age 125. The disturbance effects are also reflected in observed densities of all live trees (Fig. 7b), which spiked with an influx of regeneration in the years following the storms.

In the densely stocked red alder plot (23) at Cascade Head, ZELIG projections of total basal area tracked the observed data reasonably well (Fig. 7a). There is some divergence at the last measurement, which can be traced to the establishment and growth of Sitka spruce in the plot. Spruce was first documented in the stand at age 31 and grew rapidly thereafter. ZELIG simulated the regeneration of spruce but its growth rate was much slower than in reality. For instance, at age 55, when simulated and observed total basal area were nearly identical, the simulated data showed just 0.5 m^2/ha basal area in conifers (hemlock and spruce), whereas the observed data had 4.3 m^2/ha basal area of Sitka spruce alone. It is not known if the spruce trees in the plot were advance regeneration (present at the time of plot establishment but too small to be tagged), or if they regenerated after plot establishment. Other discrepancies are evident, as well. The density of live trees declined much more rapidly in the observed data than in the simulation; ZELIG projects a similarly steep decline but it began about 7 years later (Fig. 7b). The dbh distribution for plot 23 reflects strong differences in stem sizes of red alder (Fig. 8). In the observed data, red alder trees occur at higher densities across a narrower range of diameters than that simulated by ZELIG. In addition, all of the trees at least 50 cm dbh in ZELIG are red alder, whereas in the observed data only Sitka spruce met that threshold. Moreover, ZELIG simulated the establishment of western hemlock and scattered red cedar, neither of which appear in the observed data. Trajectories of the two site classes for this plot differed little in ZELIG because we used the same parameters for red alder for both classes.

The simulated trajectories for conifer basal area and density of large trees compares well with the observed data in plot 41 (Fig. 7). This plot is dominated by Douglas-fir, and at the time of plot establishment included a small proportion of red alder and western hemlock. The dip in basal area at age **110** in the observed data coincides with the timing of the 1981 storm mentioned previously. There was divergence in the density of both live and dead trees in the observed and simulated data (Fig. 7b), with ZELIG simulating an increase in live trees for 20 years before declining, and the observed data showing a gradual decline throughout the 60-year data record. This plot had fairly low initial tree density (less than 400 tph), likely allowing ample light for regeneration of shade-tolerant conifers in ZELIG (Fig. 8). In reality, the number of hemlock in the plot stayed nearly constant through time.

4. Discussion

Our use of ZELIG in CLAMS was not an "off the shelf" task. Despite its foundation in successional processes and prior use in the Pacific Northwest, ZELIG needed to be parameterized and calibrated for conditions unique to the Oregon Coast Range. The strategy of using multiple data sources, including simulations from the ORGANON growth-and-yield model, allowed us to calibrate ZELIG to a variety of stand types, stand ages and species mixes characteristic of the Coast Range. This was a labor-intensive effort involving numerous iterations of modifying model parameters. Through this process we blended ZELIG's ecological function with a capacity for reliable estimates of stand growth and volume in young, productive Douglas-fir forests. We pushed the model to deal with differences in site quality and a range of management practices and intensities (e.g., vegetation control and genetically

improved planting stock), which ultimately necessitated the use of a diameter-growth multiplier. Evaluating ZELIG with independent data from Black Rock and Cascade Head demonstrated that the model can accurately predict attributes for some stand types, while raising questions about its performance with others.

Simulations of seven of ten plots at Black Rock and plot 41 at Cascade Head showed that ZELIG produces reasonable and in some cases accurate estimates of basal area and large-tree density in Douglas-fir stands through the range of stand ages (40-125 years) and silvicultural treatments represented by these data. This capability was critical for the CLAMS project, given that Douglas-fir is the dominant tree species and primary commercial timber species in the Oregon Coast Range. Our results appear comparable to those from a study of a ZELIG variant parameterized for the Oregon Cascades, in which average percent critical errors (Freese, 1960) between observed and simulated values in unthinned Douglas-fir stands ranged from about 3-9% for total basal area and 6-16% for total tree density at $\alpha = 0.05$ (Garman, 2004). In addition, we found that for the majority of Douglas-fir test plots, distinguishing medium from high site classes in ZELIG resulted in a better prediction of stand attributes.

Simulations of two thinned plots at Black Rock (25 and 35) illustrated some underlying problems in ZELIG. In these plots, ZELIG lagged behind the observed data in basal area and large-tree density after the last thinning. We hypothesized three reasons for this: slower growth, higher mortality, or a difference in how the plots were thinned in ZELIG compared to reality. To examine the possibility of a difference in thinning, we did follow-up simulations that were initialized with the observed tree list after the final thinning (i.e., at stand age 63 in plot 25 and age 64 in plot 35). These simulations, while producing basal areas and large-tree densities that were higher than the original simulations, still lagged behind the observed data. This suggests slower growth rates as a likely cause. In a study of mixed-hardwood stands in Kentucky, Yaussy (2000) found that ZELIG was unable to simulate the size and number of large oak trees present in the actual stand. In our study, the tendency for slower growth was evident when we compared ZELIG to ORGANON simulations of highly productive young stands. Different combinations of growth-related parameters did not remedy this problem, so we applied diameter-growth multipliers for Douglas-fir (and for western hemlock and Sitka spruce) that were site-class specific. These multipliers brought diameter-growth rates into line with the fast-growing stands in ORGANON, and allowed us to better distinguish medium sites from high sites. The multiplier appears to have achieved its purpose (on the basis of basal area and large-tree density) for the majority of the Douglas-fir stands in our test data, but not for plots 25 and 35 at Black Rock.

Further scrutiny of the simulations for plots 25 and 35 revealed that ZELIG killed off far more trees than actually died. At the final measurement date, ZELIG had about 20% fewer Douglas-fir over 25 cm dbh compared to the observed data for plot 25, and about 10% fewer than the observed data for plot 35 (data not shown). Tree mortality in ZELIG was also higher than the observed data for the unthinned control plots at Black Rock. Thus, it appears that boosting diameter growth via the multiplier resulted in a trade-off: satisfactory trajectories of basal area and large-tree density at the expense of higher tree mortality. This would have consequences for our habitat models that incorporate snags or down wood as predictors (Spies et al., 2007b). A likely explanation for the higher mortality rate is that larger trees produced larger crowns, thus leaving less space (light) for neighboring trees which then succumb to competitive exclusion. Such density-dependent mortality in ZELIG is a function of growth rate, but does not take into account the possibility that some species may tolerate slow growth rates better than others (Wyckoff and Clark, 2002). Another consideration is the extent to which ambient (non-density dependent) mortality contributes to total mortality. Every tree in ZELIG, regardless of its size, is prone to ambient mortality - a function of maximum species longevity that is applied stochastically at every time step. The drawbacks of this simplistic approach have been addressed in reviews by Keane et al. (2001) and Monserud (2003). The limitations of the ambient mortality function were also made evident by the major wind event at Cascade Head, which dramatically altered the trajectory of the observed data (Fig. 7a-c). Because the function spreads out mortality over time with a fixed probability, it cannot adequately characterize major episodic disturbances such as windstorms or fires.

A more basic question raised by our use of diameter multipliers and the findings of Yaussy (2000) concerns the mechanisms in ZELIG that constrain diameter growth. One possibility that may need a closer look is how growth efficiencies and the modeling of leaf area interact with shade tolerance in determining a tree's competitive ability. Another explanation could be the limitations of the temperature response function. The function's parabolic shape dictates that a species' growth rate is unrestricted by temperature only at the optimum number of growing degree-days (midway between the species' minimum and maximum). As temperatures become warmer (or colder), potential growth rate is increasingly constrained. However, there is evidence that growth rates do not decline as a species reaches the warmer limits of its range, but rather plateau or continue to gradually increase in an asymptotic manner (Bonan and Sirois, 1992; Schenk, 1996). Modifying the temperature function in a gap model to reflect this growth response was proven effective in other simulations of Pacific Northwest forests (Bugmann and Solomon, 2000). In our study, Sitka spruce may be an example of a species for which the parabolic function is inappropriate. Temperatures in the Oregon Coast Range are higher than that corresponding to the function's optimum for Sitka spruce, such that its growth rate was restricted to 80% of its maximum in ZELIG. The restriction on Sitka spruce growth may be unreasonable given the relatively high productivity documented for these forests (Gholz, 1982), as confirmed by the data from plot 23 at Cascade Head where spruce showed a capacity for exceptionally fast growth. A contributing factor may be that temperature and other climate parameters in ZELIG are based on monthly averages from a single, representative location in each ecoregion. An alternative would be to use finer-scale (sub-ecoregion) environmental parameter sets.

The simulation of stand types dominated by Sitka spruce and western hemlock produced mixed results among the attributes we examined. ZELIG lagged in basal area and retained fewer live trees relative to the test data. The immediate decline in simulated live tree densities on plots 4, 7 and 8 (Fig. 7b) may indicate that hemlock and spruce are in reality more tolerant of shade and crowding than the model, as parameterized, allows. However, data from an independent chronosequence (Barnes, 1962) suggest the ZELIG simulations may be reasonable. The Barnes (1962) chronosequence was developed from data collected in the early 1930's in even-aged spruce-hemlock stands in coastal Oregon and Washington (Meyer, 1937). There were 117 plots on site-class 3 ground (comparable to the site class for plots 4, 7 and 8 at Cascade Head). Total basal area in the chronosequence averaged about 74 m^2/ha at stand age 80 and about 83 m^2/ha at age 140 (Barnes, 1962). Those values are below the conifer basal areas simulated by ZELIG for the plots at Cascade Head (Fig. 7a), thus the ZELIG values are sandwiched between the Barnes' chronosequence data and the test data. A similar pattern was apparent with total tree density. The Barnes' chronosequence averaged about 535 tph at 80 years and 284 tph at 140 years. ZELIG-simulated densities for the

Cascade Head plots ranged from 475 to 882 at age 85 and from 298 to 335 at age 140. Taken together, this evidence makes it conceivable that ZELIG simulates what could be considered "average" stand conditions in spruce-hemlock forests of the fog ecoregion. Furthermore, in the years prior to the major windstorm, ZELIG accurately predicted a lack of tree regeneration in the spruce-hemlock plots (Fig. 8), likely due to minimal light reaching the forest floor through the deep-crowned spruce and hemlock trees.

We were less satisfied with ZELIG's simulation of the red alder plot (23) at Cascade Head, even though it resulted in a fair approximation of total basal area and matched observed total tree density at the last measurement. The problems were in the simulated growth rate of Sitka spruce, as mentioned above, and the diameter distribution of red alder. ZELIG simulated a broader, flatter distribution of alder diameters than observed, evoking canopy stratification and suggesting that the alder are too shade tolerant in the model. In contrast, the observed data are consistent with red alder's status as a shade-intolerant pioneer (Harrington et al., 1994), which in pure stands typically grows as a single-layered cohort with a fairly tight diameter distribution. That said, we have observed red alder regenerating in canopy openings in the Coast Range, thus assigned it a shade-tolerance ranking of 4 in ZELIG (one rank less than the most intolerant). This ranking may have allowed smaller alders to persist within or below the dominant canopy. A logical next step would be to test alder growth with a shade tolerance rank of 5.

In plots dominated by Douglas-fir or red alder, ZELIG generally overestimated the establishment and growth of shade-tolerant understory trees. The ramification is that canopy stratification in these stand types would develop sooner than might actually occur, which would be problematic in modeling wildlife habitat that is keyed to complex forest structure (Spies et al., 2007b). The challenge of accurately simulating regeneration dynamics has been documented previously with ZELIG (Larocque et al., 2006), although in that study ZELIG under-predicted the regeneration of shade-tolerant species. Tree regeneration in the Coast Range is highly variable and its occurrence is influenced by proximity to seed sources (Schrader, 1998), herbivory (Brandeis et al., 2002) and competing vegetation (Tappeiner et al., 2001). In ZELIG, we tried to account for these factors by creating six different regeneration pathways (i.e., probability sets) that were assigned on the basis of initial stand cover type and the presence and crown class of shade-tolerant conifer species (seed sources). Comparisons with the calibration data led us to reduce substantially the regeneration probabilities; for example, the rates we used for western hemlock were 10-40% of their pre-calibrated value, depending on the pathway. However, simulations of the Black Rock data suggest that additional constraints on regeneration may be needed, such as an understory vegetation submodel or competition index, as recognized by Price et al. (2001). The flexibility of ZELIG and gap models in general provides a programming framework for addressing such challenges.

5. Conclusions

We calibrated the gap model ZELIG to simulate a wide range of forest types and stand conditions in the Oregon Coast Range. Our approach to calibrating model parameters with chronosequences of inventory data, long-term research data, and simulations from an empirical growth-and-yield model met with mixed results. Comparisons with independent data show that our emphasis on the development of commercial-aged stands of Douglas-fir was largely successful. Simulations of other species and tree regeneration were less successful, although comparisons with chronosequences suggest that our simulations are within the range of variability observed in the Coast Range. This may underscore the limitations of relying on a small number of plots from restricted geographic areas for testing a model calibrated for an entire physiographic province. It also highlights the importance of long-term research on forest stand development. We recommend further exploration and improvement of ZELIG in three key areas: (1) simulating rapid rates of conifer tree growth without the need for a diameter-growth multiplier, with particular attention to the temperature response function; (2) understanding and remedying rates of tree mortality that were higher than those observed in the independent data; and (3) developing a more robust method of modeling tree regeneration that accounts for competition with understory vegetation.

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