Modeling Effects of Overstory Density and Competing Vegetation on Tree Height Growth

Christian Salas, Albert R. Stage, and Andrew P. Robinson

Abstract: We developed and evaluated an individual-tree height growth model for Douglas-fir [*Pseudotsuga menziesii* (Mirbel) Franco] in the Inland Northwest United States. The model predicts growth for all tree sizes continuously, rather than requiring a transition between independent models for juvenile and mature growth phases. The model predicts the effects of overstory and understory vegetative competition on height growth. Our model requires attained height rather than tree age as a predictor variable, thereby avoiding the problems of site index. Site effects are introduced as a function of ecological habitat type, elevation, aspect, and slope. We used six data sets totaling 3,785 trees in 314 plots. The structure of the data and the model indicated the need for a mixed-effects, nonlinear modeling approach using maximum likelihood in a linear differential equation with a power transformation. Behavior of the model was analyzed using a state-space approach. Our results show that both overstory and understory density affect height growth, allowing a manager to make informed decisions about vegetation control. FOR. SCI. 54(1):107–122.

Keywords: differential equations, competition, density, mixed-effects models, maximum likelihood, state-space approach, Douglas-fir, site index

WE PRESENT AND EVALUATE an individual-tree height growth model for Douglas-fir (*Pseudotsuga menziesii*) in the Inland Northwest. We developed this model using a collection of modeling strategies that answer or circumvent a number of challenges that have traditionally beset individual-tree height growth model construction.

A major use of models of stand dynamics is to estimate and predict the effects on stand growth of stand density, which is the major factor that the forest manager can manipulate in the developing stand. The development of models that represent forest dynamics has been hampered by the modest detail of data available for modeling height increment.

Competition effects have rarely been considered in modeling top height growth, because top height growth is assumed to be relatively independent of stand density across the range of operational densities (Clutter et al. 1983, Smith et al. 1997, Husch et al. 2003). However, this assumption is not necessarily defensible in natural stands or when trees are competing strongly. Competition during the early years, which is a normal condition in natural and selection forests, reduces height increment and postpones the age of maximum growth-rate by up to 50–100 years in Europe (Assmann 1970). During the juvenile period, reducing the density of competing vegetation plays a critical role in early forest growth (Daniel et al. 1979, Smith et al. 1997). Furthermore, several authors have reported stand density effects on height growth of older trees (Gaiser and Merz 1951, Lloyd and Jones 1983, MacFarlane et al. 2000). Also, some authors have reported positive (i.e., increasing) effects of density on both height and diameter growth of juvenile trees (e.g., Scott et al. 1998, Woodruff et al. 2002, Kerr 2003).

Some models do include density effects on height growth. For example, adjustments of site index curves due to density have been implemented in some areas of forest height growth modeling (Alexander 1966, Alexander et al. 1967, Flewelling et al. 2001). The influence of stand density on height growth models was recognized in other modeling efforts, but site index was still used as the driving variable (Alexander 1966, Alexander et al. 1967, Cieszewski and Bella 1993, Flewelling et al. 2001, Hall and Bailey 2001, Uzoh and Oliver 2006). A notable exception is the Prognosis model (Stage 1973, Wykoff et al. 1982), which includes reduction of the height growth through a relation of height to diameter growth without using site index.

Most models that include the effects of understory density on height increment are focused on juvenile trees. The greatest potential for improving growth rates in forests is during the early stages of establishment before canopy closure (Mason et al. 1996, Mason 2001, Watt et al. 2004). Accurate modeling of the development of recruited and juvenile trees is crucial for simulation models to achieve a consistent simulation output (Golser and Hasenauer 1997), and development of accurate juvenile tree growth models sensitive to competition would enable managers to make

---

Christian Salas, Departamento de Ciencias Forestales, Universidad de La Frontera, Chile, and School of Forestry and Environmental Studies, Yale University, 360 Prospect St., New Haven, CT 06511-2189—Phone: (203) 432-5126; Fax: (203) 432-3809; christian.salas@yale.edu. Albert R. Stage, US Forest Service Rocky Mountain Experiment Station, Moscow, ID 83843—astage@moscow.com. Andrew P. Robinson, University of Melbourne, Melbourne, Victoria 3010, Australia—a.robinson@ms.unimelb.edu.au.

Acknowledgments: We thank the Inland Northwest Growth and Yield Cooperative (in the person of Dr. John Goodburn), Dr. Robert Monserud (US Forest Service), and the Intermountain Forest Tree Nutrition Cooperative (in the person of Peter Mika) for providing the data used for this research, as well as details about the sampling procedure. The research was supported by the Rocky Mountain Research Station (US Forest Service) in Moscow, ID, and the Inland Northwest Growth and Yield Cooperative in Missoula, MT. Gratitude is also extended to Lauri Mehtätalo, the associate editor, and two anonymous reviewers, whose comments improved an earlier draft of this article. This research was mostly conducted while C. Salas was a graduate student of the Department of Statistics, University of Idaho, Moscow, ID.

Manuscript received February 2, 2007, accepted July 23, 2007

informed decisions regarding vegetation management (Watt et al. 2004).

Some current juvenile models have omitted competing vegetation effects (see, e.g., Nigh and Love 1999). Models that account for competing vegetation, for example, Mason et al. (1996), Loveall (2000), Mason (2001), Watt et al. (2004), and Westfall et al. (2004) are focused on plantations, where clear cutting is the most common harvesting method. Clear cutting promotes juvenile development without overstory effects, so the models cannot be applied to other harvesting systems or to uneven-aged or mixed stands. Besides, under intensive forest management, treatments of competing vegetation, and spacing are more homogeneous. Thus, their generally uniform growth can be modeled at either a stand- or individual-tree level of organization.

Modeling juvenile height increment has been hampered by the correlation between quantity of competing vegetation and height increment of the subject species in natural stands. Good sites produce both more competing vegetation and more height increment than do the poorer sites. If the application of the prediction of height increment is for undisturbed natural stands and is calibrated from a random sample of the population, then the aliasing of quantity of vegetation for site quality does not bias that prediction. Our objective, however, is to model the effects of modifying competition so the aliasing would be a major problem. To determine an independent effect of competition, therefore, requires data in which this aliasing of competition variables for site quality is nullified. The necessary independence can be obtained by the experimental design of direct control of the competing vegetation.

Our model is intended for imbedding in a model that has an individual-tree level of organization, with output integrated to the stand level (Stage 2003). Models of this structure often calculate height increment in two or three stages—as attained height of new regeneration at a fixed time after disturbance, as subsequent height increment of juvenile trees, and finally, as height increment of larger trees.

In this general framework, estimates from juvenile- and older-tree models usually give different predictions for the same conditions. Many current juvenile height growth models have been built using only juvenile trees to be used up to the point at which large tree height growth models become applicable. However, in most cases the predictions from juvenile and older tree models at the same point (e.g., at the same age or height level) are different. Wykoff et al. (1982) proposed a smooth transition to accommodate this inconsistent model behavior, when using juvenile and older tree height growth models. It would be preferable to have one model that provides consistent projections for all phases of growth.

Empirical analysis of height growth has usually used for forward finite difference models. In such models the period of observation used for fitting height growth models affects the predictions. Several period lengths have been used for fitting height growth models, mainly between 5 and 10 years (e.g., Stage 1973, Wykoff et al. 1982, Hann and Ritchie 1988). A user who needs to predict increment for a period length different from the length of the calibration period must interpolate. Different interpolation methods have been developed to deal with this issue (MacLean and Scott 1987, Ochi and Cao 2003, Cao 2004) but all of them are ad hoc “fixes” and do not account for biological behavior. Instead, using differential equations (i.e., any equation that involves differentials or derivatives, Franklin 1944) will always result in compatible estimations regardless of the period length, so that complex interpolation methods are unnecessary. Another important advantage of using differential equations is their flexibility, allowing us to combine data sets with increments measured at intervals of varying length. An interesting application of this combination of diverse sources of data was shown by García (2005). Then, using these data we can fit a model based on a differential equation, and when we want to predict, we integrate the model over the period of interest. If changes in the independent variables are simulated by forward difference models, their effect is assumed to follow their average change during the period used to calibrate our differential equation of height increment. Our objectives are to develop a biological height growth model incorporating all competing vegetation effects (trees, shrubs, forbs, and grasses), also representing growth of trees of all sizes, which does not depend on length of period of observation, and recognizing the statistical implications of analyses of data in which sampled trees are clustered in plots.

We first hypothesized a model consistent with our understanding of the growth of Douglas-fir. At this stage, we used parameters from published models for height increments of dominant trees absent any consideration of competition. Then we postulated a range of parameters of the competition components of our hypothesized model to assure that the proposed mathematical model had sufficient flexibility to encompass the uncertainty of our expectations (Salas et al. 2005). Only then did we introduce data into the model. In our initial analyses we used two data sets deemed to have the strongest basis for representing competition effects—one consisting of juvenile trees with experimentally controlled understory competition and the other consisting of trees 14–50 m in height drawn from undisturbed stands of known levels of stocking. These analyses narrowed the choice of expressions for competition and informed the choice of parameters to be considered random in the mixed-effects statistical model (Salas 2006). Four additional data sets then were added into the analyses to strengthen the representation of trees in the less-than-dominant crown positions. In the last step the behavior of the final model was explored.

Data

Study Area

Our data come from forest stands located in the Inland Northwest region of the United States. This is essentially the lower portion of the Interior Columbia River Basin, which is in the coterminous United States East of the crest of the Cascade Mountain Range (Hessburg and Agee 2003), covering states of Idaho, western Montana, and eastern Washington. The Inland Northwest landscape has much variation owing to great variety in climate, geology, landforms and topography, plants and animals, and ecological processes (Hessburg and Agee 2003). Over broad areas in the Inland Northwest, rugged mountainous topography, contrasting geologic substrates, and a highly variable maritime influence from the Pacific coast combine to create a wide variety in species composition and productivities (O'Hara et al. 1996). Existing stand structures are strongly influenced by a long history of partial harvests and impacts of pests on particular species in mixed-species stands.

Measurements

Our analysis involved six data sets. Not all required variables in the model were observed for all of these. When a variable was missing, it was estimated from other sources. However, estimates of particular parameters in the model were based on only the subsets of the data with field-measured values of the associated variables. Of the six data sets, only the Inland Northwest Growth and Yield Cooperative (INGY) sampling design (which contains juvenile trees and is explained below) would have permitted subject-tree-centered (distance-dependent) measures of competition. Therefore, we computed all competition indices as average for the entire stand. As stand-level variables, they also are subject to less sampling error than more localized indices. Data with intermediate sized trees come from the Intermountain Forest Tree Nutrition Cooperative (IFTNC) of the University of Idaho. Of the four IFTNC data sets, only two, the Forest Health Trial (FHT) and Klickitat included observations of understory vegetation. Data with the largest sized trees come from the stem analysis data measured by Monserud (1984). Further details about his measurements and our estimates of missing variables are explained below.

1. INGY. The most extensive and detailed data for juvenile trees come from the "Small Tree and Competing Vegetation" study established during 1998 by INGY. In this study of 23 stands, each stand was selected to represent a homogeneous combination of site quality, overstory density, and understory competition. Within each stand, seven permanent plots were established. Each plot comprised a circular 1,816 m^2 (0.46-acre) plot in which large trees ($\geq$26.7 cm [10.5-in.] dbh) were measured, a circular 1,052 m^2 plot (0.26-acre) in which medium trees (9.1–26.7 cm [3.6–10.5 in.] dbh) were measured, and six circular 28 m^2 plots (0.007-acre) in which small trees (0.15–0.3 m [0.5–1 ft] in height to 26.7 cm [3.5 in.] dbh) were measured. Furthermore, each small-tree plot has a 1-m^2 (0.0002-acre) plot in which understory vegetation was measured. Three vegetation treatments (herbicide: T1, control (i.e., no application), T2, single application; and T3, repeated application) were applied randomly to each measurement unit (large tree plot) within an installation. Treatments 1 and 3 were randomly assigned to two plots each, and treatment 2 was assigned to three plots, for a total of seven plots. The goal of the treatment was to reduce the foliar biomass of understory vegetation (INGY 1999) and allow growth of small trees without competing vegetation (i.e., shrubs, forbs, or grasses), because it has been reported that like tree growth increases in good sites, levels of understory increase as well (Stage and Boyd 1987, Walstad and Kuch 1987). Several variables were measured in each plot at different years (for more details, see INGY 1999).

   Crown competition factor (CCF) (Krajicek et al. 1961) of each individual tree was estimated using the CCF models fitted by Wykoff et al. (1982) according to each species and dbh range. For species without models, the grand fir (*Abies grandis*) equation was used. Stand basal area (G), CCF, and number of trees per hectare (N) were expanded to a per hectare basis and summed over the subplots. Understory cover (UCOVER), understory height (UH), and understory crown volume (UCV) were computed as understory variables. UCOVER was ocularly estimated in each of the understory plots. UH was computed by averaging the height of the understory in each of the understory plots. UCV was computed by multiplying the average crown length of the understory by the crown area (UCOVER computed on area units). UCOVER, UH, and UCV were computed on the basis of measurements in each understory plot, and as this measurement was established at the center of the small tree plot, it was assumed to represent the understory variables at the small tree plot level.

2. Monserud. The data for the largest trees come from the site index study of Douglas-fir by Monserud (1984) in the same region. Monserud (1984) selected 135 stands (plots) to cover a wide range of ages and the five major habitat series that contain Douglas-fir in the northern Rocky Mountains. He used stem analysis data for fitting his height growth equations, but furthermore he recorded overstory information for each stand for which three dominant trees were selected for stem analysis. This information was recorded in 1976. Each plot consisted of three angle count sample points with a basal-area factor of 20 ft^2/acre (4.6 m^2/ha).

   Because Monserud (1984) only measured traditional variables used in site index studies (recording neither understory variables nor small tree variables), the past and current (in 1976) overstory (basal area [G], trees per hectare, and CCF) and understory variables (UCOVER and UCV) needed for our modeling were estimated using the Shrub and Cover extension (Mouer 1985) of Prognosis (Stage 1973, Wykoff et al. 1982).

3. Forest Health Trials. FHT plots were established in managed, second growth Douglas-fir stands in the same region, but the aim here was to study the influence of soil parent material on the nutrition and health of established conifer stands (Garrison et al. 1997b, Moore and Mika 1997). These study sites were established between 1994 and 1996, and plots were 0.2 ha in area.

4. Klickitat. This data set comprises study sites installed in the Klickitat area of South-Central Washington to

assess response to fertilization (Garrison et al. 1997a). Only unfertilized control plots were used. These study sites were established in 1990, and plots were 0.4 ha in area.

5. Douglas-fir Trials (DFT). The DFT data set is from the unfertilized control plots for a fertilization experiment established in second-growth, even-aged, managed Douglas-fir stands in the Inland Northwest region (Moore et al. 1991). These study sites were established between 1980 and 1982, and plots were 0.04 or 0.08 ha in area.
6. Umatilla. These plots are located in the Umatilla National Forest (northeastern Oregon), in second-growth Douglas-fir and grand fir stands (Garrison et al. 2000). These study sites were established in 1991, and plots were 0.112 ha in area. Whereas the previous three data sets are intermediate tree sizes, Umatilla has juvenile trees.

The last two data sets unfortunately lacked understory observations. Therefore, we estimated them from the Shrub and Cover Extension as described for the Monserud data set. Stand characteristics for each data set are summarized in Table 1.

For each tree of the data, a periodic height increment and its period were computed. To ensure that the juvenile trees in the INGY data set had fully responded to the treatment of competing vegetation, only observations with a measured period greater than 5 years were used. (Dennis Ferguson, pers. comm., US Forest Service, Jan. 9, 2006). Only the last period of stem analysis data (Monserud) was used because the stand data collected at time of felling could not be back-dated reliably for more than one period. Our data cover a wide range of heights and height growth for Douglas-fir (Table 2).

The periodic annual height increment (pai) shows a wide range of competition, with site quality, weather, and insects/disease (among others) influencing the tree growth. However, the general trend of pai is according to the biological growth of trees (Assmann 1970, Vanclay 1994, von Gadow and Hui 1998, Zedaker et al. 1987). Figure 1 shows the data segregated by each dataset.

Modeling Strategy

We first develop the biological structure of our model in terms of the interaction of competition with the parameters of the height growth model. Then we define the statistical model components and the computational procedures for estimating the parameters.

Height Growth Model

We used a generalization of the von Bertalanffy (1957) growth model (a generalization that allows one of the parameters to be estimated, instead of being held constant as in von Bertalanffy 1957), a model also studied by Richards (1959) on plant growth and by whose name it has become known to American researchers (Zeide 1993). This is a

Table 1. Stand sample variables summary for each data set

Data set and statistic	N (trees/ha)	G (m^2/ha)	d_g (cm)	CCF (%)	LAI (m^2/m^2)
DFT (99 plots)					
Minimum	222.3	12.9	13.3	70.0	2.2
Maximum	1,630.2	60.8	41.7	261.0	5.0
Mean	658.4	32.0	25.9	156.7	3.3
SD	286.9	9.9	5.4	44.2	0.6
FHT (26 plots)					
Minimum	247.0	7.1	8.7	46.0	1.6
Maximum	3,877.9	67.7	49.9	282.0	6.1
Mean	932.0	23.6	20.6	116.8	3.7
SD	815.1	13.6	8.6	59.1	1.0
INGY (55 plots)					
Minimum	0.0	0.0	0.0	0.0	0.0
Maximum	198.7	17.0	40.1	61.0	2.4
Mean	64.6	4.5	19.1	17.2	0.6
SD	67.1	5.3	14.0	19.6	0.7
Klickitat (6 plots)					
Minimum	321.1	37.6	25.9	160.0	2.1
Maximum	1,111.5	65.7	39.5	284.0	3.4
Mean	662.8	46.2	30.7	212.5	2.8
SD	260.2	12.5	5.0	54.0	0.5
Monserud (118 plots)					
Minimum	234.7	8.4	7.9	41.0	1.6
Maximum	3,542.0	66.9	41.0	350.0	5.9
Mean	1,090.1	36.0	22.2	158.2	2.9
SD	620.9	12.9	6.1	58.0	0.8
Umatilla (10 plots)					
Minimum	790.4	0.5	2.3	3.0	0.1
Maximum	1,383.2	10.6	11.1	62.0	1.3
Mean	1,039.9	3.5	5.4	20.7	0.5
SD	183.9	4.1	3.5	22.4	0.5

d_g = quadratic mean diameter.

Table 2. Tree sample variables summary by data set

Data set and statistic	h_0 (m)	h_1 (m)	Period (years)	pai (m/yr)	BAL (m^2/ha)
DFT (1995 trees)					
Minimum	6.3	7.2	8.0	0.0	0.0
Maximum	34.6	37.8	8.0	0.6	59.5
Mean	19.0	21.1	8.0	0.3	19.4
SD	4.8	4.9	0.0	0.1	11.4
FHT (336 trees)					
Minimum	1.3	2.1	4.0	0.0	0.0
Maximum	45.4	50.5	8.0	0.9	57.6
Mean	13.7	16.8	7.7	0.4	11.9
SD	7.7	8.0	1.0	0.2	9.2
INGY (786 trees)					
Minimum	0.2	0.2	5.0	0.0	0.0
Maximum	5.8	8.2	6.0	0.7	17.0
Mean	1.2	2.1	5.5	0.2	6.2
SD	1.1	1.8	0.5	0.2	5.4
Klickitat (123 trees)					
Minimum	13.8	14.5	6.0	0.1	0.0
Maximum	33.4	37.1	6.0	0.8	61.3
Mean	23.6	26.5	6.0	0.5	27.2
SD	4.4	4.8	0.0	0.1	15.8
Monserud (377 trees)					
Minimum	14.1	16.3	6.0	0.0	0.0
Maximum	48.8	49.4	19.0	0.5	65.5
Mean	31.3	33.0	9.9	0.2	14.9
SD	5.9	5.5	1.0	0.1	10.8
Umatilla (168 trees)					
Minimum	1.4	2.2	8.0	0.1	0.0
Maximum	9.0	13.4	8.0	0.8	10.6
Mean	2.9	7.2	8.0	0.5	2.2
SD	1.6	2.0	0.0	0.1	3.2

h_0 = initial height; h_1 = height measured at the end of the period.

nonlinear model used successfully in forestry for modeling growth in terms of several variables, mainly in its integrated form (e.g., Pienaar and Turnbull 1973, Pienaar and Shiver 1984, Zeide 1993, Hall and Bailey 2001), but also used in its differential form (e.g., García 1983, Valentine 1997). The Richards model comes from a linear differential equation with a power transformation (García 1983). The linear differential equation with a power transformation is

$$\frac{dh^c}{dt} = b(a^c - h^c). \qquad (1)$$

If we analytically integrate a differential equation, we will obtain a yield (i.e., cumulative growth) equation. Then, integrating Equation 1 between t_0 and t_1 gives the height at t_1 (that is, h_1), in terms of h_0 and the period length $t_1 - t_0$ (García 1979, 1983, Rennolls 1995). The integral yields

$$h_1 = a\{1 - [1 - (h_0/a)^c]\exp[-b(t_1 - t_0)]\}^{1/c}. \qquad (2)$$

This expression could be called the yield function, assuming the definition of yield as accumulated growth as per Zedaker et al. (1987) and Vanclay (1994). a, b, and c are parameters to be estimated. a is the upper asymptote or maximum level of yield, b is the growth parameter (also has been called a scale parameter, which governs the rate of change, by Schabenberger and Pierce 2002), and c is a shape parameter. The value of $(h_1 - h_0)$ will always be of the same sign as $(t_1 - t_0)$ if b and c are positive. As pointed out by García (1983), $t_0 = h_0 = 0$ in most forestry applications. Then, the yield function becomes the so-called Chapman-Richards (Pienaar and Turnbull 1973, Pienaar and Shiver 1984, van Laar and Akça 1997, von Gadow and Hui 1998) function,

$$h_1 = a[1 - e^{-b(t_1)}]^{1/c}. \qquad (3)$$

As a function of age, Equation 3 is useful mainly for purposes of modeling forest plantations, where the age is easily determined. However, exact age is difficult to determine in natural stands. Breast height age is usually used but is not useful for modeling growth of small trees, because they do not have dbh. Besides, models for predicting growth should not have age as a primary variable (Spurr 1952). Another important feature of Equation 2 is that it permits different length of periods of observation when fitting the model, and use of the differential equation (Equation 1) makes it possible to obtain the instantaneous growth based on height instead of age.

Incorporating Competition Effects

Increment can be increased by increasing a or b in Equation 2. We will describe introducing competition into the b parameter although a similar modification of a was also evaluated. Competition due to overstory (large trees) and understory are represented by three variables in our proposed model [1]. Equation 2 is modified by having the b parameter depend on competition, which we denote as b'. The modified growth parameter is the expression

$$b' = b\left[\beta_4 - \frac{1}{1 + e^{\theta}}\right], \qquad (4)$$

$$\theta = \beta_0 + \beta_1 \mathrm{OVER}_0 + \beta_2 \frac{\mathrm{OVER}_0}{\sqrt{h_0}} + \left(\frac{\mathrm{UH}_0}{h_0^2}\right)\beta_3 \mathrm{CVEG}_0, \qquad (5)$$

where b is a parameter related to the maximum growth rate, OVER_0 is a variable that represents the overstory competition (e.g., it could be CCF, BA, or basal area per unit area of trees larger than the subject [BAL]), UH_0 is the average height of the understory, and CVEG_0 is a measure of the amount of competing vegetation (e.g., it could be understory cover or understory crown volume). Note that the 0 subscript of the variables means those that are measured at the beginning of the period. The parameters to be estimated are β_0, β_1, β_2, β_3, and β_4.

This term (b') was created on the basis of a "logistic mirror" relation of the reduction of the potential (i.e., without competition effect) height growth. If $\beta_4 = 1$, b' equals b multiplied by a value between zero for very small θ and approaches unity for θ large. Thus, growth will increase for positive terms in Equation 5. This behavior allows some range where this potential is almost independent of density. This formulation is different from the formulation used by Golser and Hasenauer (1997), where height growth was very sensitive to low levels of competition. Our hypothesis is that, at least in some range of low densities, height growth should not be strongly affected by competition and that at

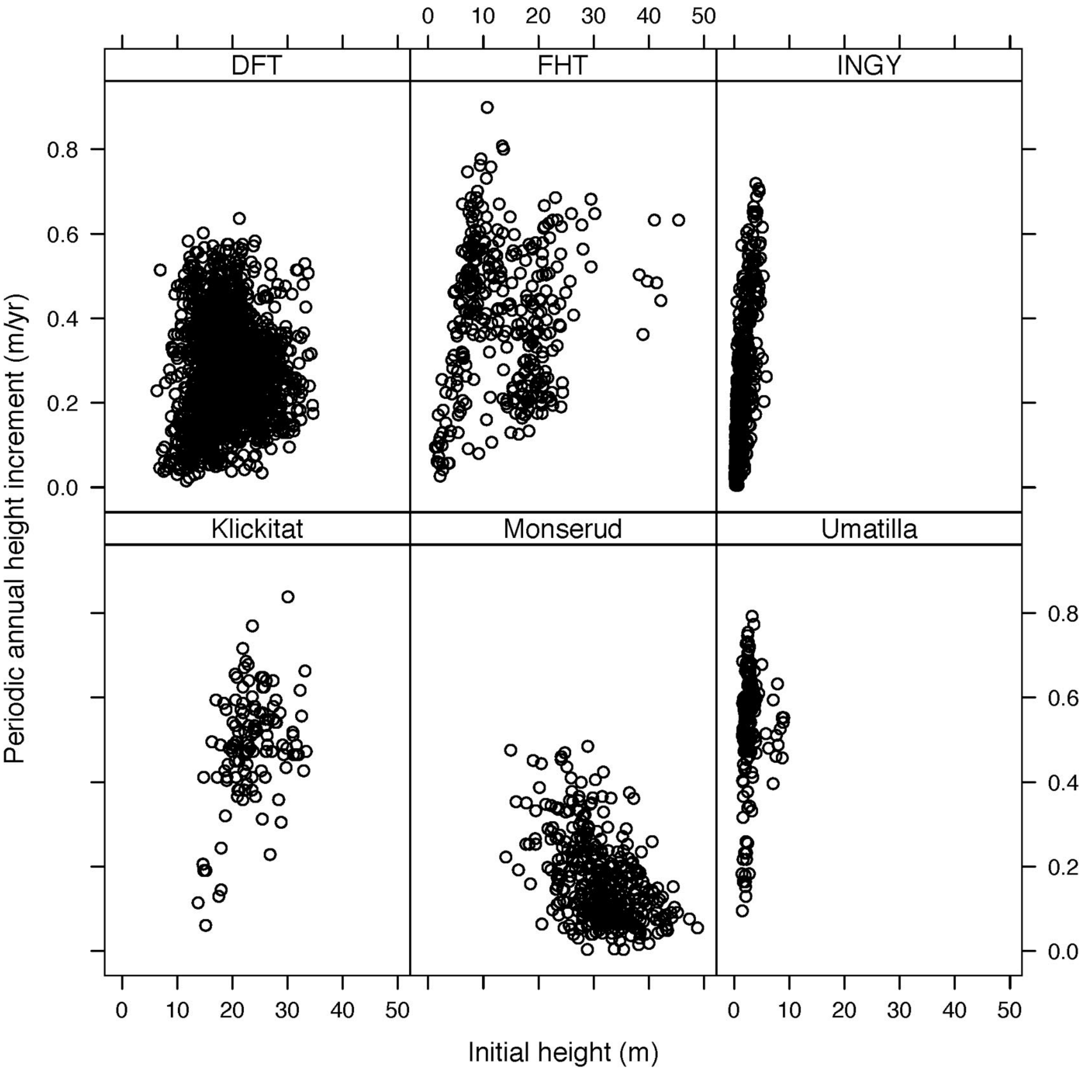

Figure 1. Periodic annual height increment for Douglas-fir in the Inland Northwest by data set.

extremely high levels of competition, increment is again less sensitive to increasing competition.

The term b' represents a reduction of the growth parameter due to overstory and understory competition. Variables representing the overstory effect (through OVER) were screened as a quadratic effect for leaf area index (LAI), CCF, G, and BAL. Although the intent of this transformation was to allow curvature of the effect of OVER variables, it also allowed for a positive effect of stocking for some portions of the span of the variable. A similar effect was successfully modeled by Ferguson et al. (1986) for Douglas-fir, grand fir, and subalpine fir (*Abies lasiocarpa*). Growth is also reduced by competition from understory vegetation; see, e.g., Mason et al. (1996) and Watt et al. (2004) (among others). The height ratio (UH/h_0^2) forces the reduction from understory vegetation to be large only for juvenile trees and less so for bigger trees because the ratio will be much lower for larger trees.

We also introduced overstory density and competing vegetation into the asymptote (a) using an expression similar to b'. However no significant improvement was achieved. We therefore limited competition effects to the growth parameter (b) and reserved the asymptote (a) for site productivity (quality) effects.

Statistical Model

Our data set is hierarchical, because for all the trees within a plot, we are using the same stand value of OVER. Schabenberger and Pierce (2002) classify this design as clustering data through hierarchical random processes. Mixed-effects models are quite suitable for this kind of design. We consider the plot (in each location) as the random factor (i.e., group). Unfortunately, the small-plot level could not be used as a random effect because in some of the plots the number of trees was too small to get convergence.

To ease notation, define the n-dimensional response vector $\mathbf{Y}$ by an arrangement of $h_{(i,j,k+\text{period})}$, i.e., the height at the end of the period (since the kth time, period $= t_1 - t_0$) at the jth plot in the ith tree. Then, the nonlinear mixed effects model can be expressed as

$$\mathbf{Y} = \mathrm{f}(\mathbf{X}\beta, \mathbf{Z}\mathbf{b}) + \epsilon, \tag{6}$$

where, using a mix between Laird and Ware (1982) and Hall and Bailey (2001) notation, f is a nonlinear function, β denotes a $P \times 1$ vector of unknown population (i.e., fixed) parameters, X is a known $n \times p$ design matrix linking β to $\mathbf{Y}$, $\mathbf{b}$ denotes a $k \times 1$ vector of unknown individual effects (i.e., random), and $\mathbf{Z}_i$ is a known $n_i \times k$ design matrix linking $\mathbf{b}$ to $\mathbf{Y}$. The ϵ vector is independently distributed as $\mathcal{N}(\mathbf{0}, \mathbf{R})$ (normal with mean $\mathbf{0}$ and covariance matrix $\mathbf{R}$), and the random parameters $\mathbf{b}$ are also distributed $\mathcal{N}(\mathbf{0}, \mathbf{D})$ (normal with mean $\mathbf{0}$ and covariance matrix of the random effects $\mathbf{D}$).

We fit all models using maximum likelihood (ML) theory, assuming a normal probability density function for the residuals. Restricted maximum likelihood (REML) estimation has gained popularity among statisticians, because compared with a ML estimator, the REML procedures take into account the loss in degrees of freedom resulting from estimating fixed effects in the model (Harville 1977); therefore, variance components are estimated without being affected by the fixed effects (McCulloch and Searle 2001). For those and other reasons, they have come to be preferred in general (Gregoire and Schabenberger 1996). Nevertheless, we did not find any apparent difference in the estimated random effects between the ML and REML estimators. Therefore, we prefer to use the simpler ML estimator, which allows us direct comparison between models with different fixed effects. Based on the comparisons conducted by Dennis et al. (2006) and Staples et al. (2004) that showed better performance of REML over ML estimators when fitting a nonlinear model using an autoregressive process (linear mixed-effects model), we think that important differences may be found when fitting linear mixed-effects models but not when using nonlinear models. Whichever definition is adopted, note that REML does not define estimates of fixed effects, because all REML methods are designed to be free of the fixed-effects portion of a model (McCulloch and Searle 2001).

We used the open-source statistical environment R (R Development Core Team 2006), using the nlme package (Pinheiro and Bates 2000). We compared models with the Akaike information criterion (AIC) (Akaike 1973).

Variance functions were used to model the variance structure of the within-group errors using covariates (Pinheiro and Bates 2000). All of the models were fitted allowing a different SD for the error term per stratum (each data set), as

$$\mathrm{Var}(\epsilon_{ijk} \mid \mathbf{b}_j) = \sigma^2 g^2 \ (\mu_{ijk}, \mathbf{v}_{ijk}, \delta), \tag{7}$$

where $\mu_{ijk} = \mathrm{E}[y_{ijk} \mid \mathbf{b}_j]$, $\mathbf{v}_{ijk}$ is a vector of variance covariates, δ is a vector of variance parameters, and $g(\cdot)$ is the variance function, assumed to be continuous in δ (Pinheiro and Bates 2000). Then, this represents a variance model with different variances for each S-stratum (i.e., each data set),

$$\mathrm{Var}(\epsilon_{ijk}) = \sigma^2 \delta^2_{S_{ijk}}, \tag{8}$$

corresponding to the variance function

$$g\ (S_{ijk}, \delta) = \delta_{S_{ijk}}. \tag{9}$$

To achieve identifiability, as recommended by Pinheiro and Bates (2000) we imposed the restriction that $\delta_1 = 1$.

Fitting approach

The complexity of the model and diversity of the data sets precluded estimating optimum values of all parameters simultaneously. Our fitting approach, which paralleled that of Salas (2006), consisted of the following five stages.

- Screen choice of OVER and CVEG.
- Estimate b and c.
- Estimate a as a random parameter and model a as a function of site variables.
- Estimate parameters of understory variables conditional on estimated asymptote $\hat{a}$ and with β_4 as random parameter.
- Estimate remaining parameters (β_0, β_1, and β_2) conditional on previous parameter estimates.

Screen Choice of OVER and CVEG

In our initial modeling, only the INGY and Monserud data sets were available and used. We first fitted the traditional (i.e., without density effects) model (Equation 2) allowing a to be the set of random parameters unique for each plot (also called "local" parameters by García 1983). To assess the forestry predictor variables to be included in our proposed height growth model (that incorporates density effects), Salas (2006) fitted different variants using the same two data sets. These variants used different combinations of both OVER and CVEG. The OVER variable was one of the following: crown competition factor (CCF) (Krajicek et al. 1961), stand basal area (G), trees per hectare (N), and leaf area index (LAI). Either understory plot cover (UCOVER) or understory crown volume (UCV) was used as the CVEG variable. Salas (2006) obtained best fit using G and UCOVER as OVER and CVEG variables, respectively.

These analyses reported by Salas (2006) showed that the ocular UCOVER fit better than the more complex UCV. They also showed that stand basal area (G) was at least as effective as the other, derived, variables for overstory competition. However, the quadratic expression for overstory competition proved to have a critical point (28.6 m^2/ha) well within the range of stand basal areas. Apparently the aliasing of stand stocking for site quality we expected in juvenile tree data was present in the Monserud data for older trees as well. Adding competition variables improved the likelihood over the base model (Equation 2) with the same random parameter a (likelihood ratio test $P < 0.0001$).

Substitution of stand basal area by basal area in trees larger in diameter than the subject tree (BAL) appeared to be a way of reducing the inherent correlation between natural stand stocking and site quality. However, the Monserud data was composed of mostly dominant trees with little range of BAL. Therefore, we sought additional data sets encompassing a sample across all sizes of trees within each stand and, by virtue of previous thinning, might have less aliasing of stocking for site quality. These additional data sets (DFT, FHT, Klickitat, and Umatilla), which were detailed above, were supplied by the Intermountain Forest Tree Nutrition Cooperative. Whereas stand-level basal area appeared to be related to site productivity in the undisturbed stands sampled by Monserud, BAL is an individual tree-level attribute for which the distribution is determined by the rules for sample tree selection within the stand and past stand density management. Hence, although its upper limit may be determined by the maximum basal area for the site, its actual distribution reduces the aliasing of basal area for site productivity. Furthermore, switching from basal area to BAL also improved the log-likelihood of the model (lower AIC). Therefore, our model uses BAL (basal area in larger trees) as the OVER variable and UCOVER (understory cover) as the CVEG variable in Equation 4.

Estimating b *and* c

Parameters b (Equation 4) and c (Equation 2) represent, in our formulation, parameters unaffected by density. Thus, we selected a subset (12 trees) of Monserud's dataset, which comprises the sample trees in the better sites studied by Monserud (1984) and without notable past suppression. Then, we fitted the yield model without density variables (Equation 2), using nonlinear mixed-effects, allowing a as random parameter. Through this process, we obtained the estimates $\hat{b} = 0.02018$ and $\hat{c} = 0.73708$.

Estimating the Asymptote a

Our objective at this stage was to incorporate effects of site quality using the random parameters as indicators of effects common to all the trees on each plot. Only the Monserud data set was suitable for this purpose because it contained the oldest trees growing without density control. Because site factors could operate either through the asymptote a or through the growth parameter b (i.e., the parameters of Equation 2), we tested several combinations of random parameters for our proposed model in Equation 2. The best fit was achieved with a as random parameter.

The next step used the set of asymptotes (random parameters) from each plot as variables to be predicted from site factors. Two submodels to predict these random parameters (asymptotes) were compared. One predicted the a parameters from site index. The other used slope, aspect, elevation, and habitat type (called the site variables model). The productivity model proposed by Stage and Salas (2007) as the mathematical form gave the better fit to the asymptotes. This submodel (Table 3) for a then was inserted in Equation 2 for all subsequent analysis and prediction.

Estimating Parameters of Understory Variables

β_3 and β_4 were estimated using only those data sets for which the understory variables were measured in the field (the INGY, FHT, and Klickitat data sets). By holding the asymptote of the height growth model as predicted by the site variables model for each plot and keeping b and c at their previously estimated values, the height growth model was fitted using mixed-effects models allowing β_4 as the random parameter. The estimates for β_3 and the set of β_4 values were saved.

We examined the relationship between the random parameters β_4 and several stand and site variables. We fitted the site variable model of Stage and Salas (2007) to try to predict those random effects; however, we did not find any statistically significant improvements in the fitted model compared with just the population parameter estimate (i.e., average) of β_4. Therefore, we use the mean value of the parameter estimates of β_4 for subsequent analyses.

Estimating Remaining Parameters

At this final stage, we used all six data sets to estimate β_0, β_1, and β_2 in the complete height growth model (i.e., Equation 2 having b as b' in Equations 4 and 5) using generalized nonlinear squares. The asymptote of the model was as predicted by the site variables model, β_4 was held at the mean of the random parameters as explained above, and

Table 3. Linear model of asymptote using site variables

Parameter	Estimate	SE	t value	P value
(Intercept)	2.661e + 01	1.891e + 01	1.408	0.163
Habitat class 2	−4.013e + 00	2.481e + 00	−1.617	0.109
Habitat class 3	−1.911e + 00	2.370e + 00	−0.807	0.422
Habitat class 5	3.409e + 00	1.541e + 00	2.213	0.029
Habitat class 6	5.194e + 00	1.105e + 00	4.700	8.34e − 06
Habitat class 7	6.030e + 00	1.128e + 00	5.347	5.67e − 07
Habitat class 8	3.800e + 00	1.442e + 00	2.635	0.01
EL	2.672e − 02	3.104e − 02	0.860	0.392
EL^2	−1.023e − 05	1.230e − 05	−0.831	0.408
SL	8.528e + 00	4.564e + 00	1.865	0.065
SL cos(ASP)	2.356e + 00	2.192e + 00	1.073	0.286
SL sin(ASP)	5.493e + 00	2.220e + 00	2.471	0.015
SL ln(EL)	−1.279e + 00	6.959e − 01	−1.835	0.070
SL ln(EL) cos(ASP)	−3.603e − 01	3.308e − 01	−1.090	0.279
SL ln(EL) sin(ASP)	−8.268e − 01	3.373e − 01	−2.448	0.016
SL EL^2	3.330e − 07	2.392e − 07	1.391	0.167
SL EL^2 cos(ASP)	1.194e − 07	1.012e − 07	1.180	0.241
SL EL^2 sin(ASP)	2.470e − 07	1.124e − 07	2.196	0.030

All parameters and statistics are in metric units. Residual SE = 3.813 on 100 d.f.; multiple R^2 = 0.4976; adjusted R^2 = 0.4122; F statistic = 5.825 on 17 and 100 d.f.; P = 5.088e − 09. Habitat class codes according to Wykoff et al. (1982, p. 66). SL = slope (%/100); EL = elevation (m); ASP = aspect in degrees clockwise from north. Treatment contrasts are used for habitat class.

the parameter estimate for the understory variable ($\hat{\beta}_3$) was kept constant. Understory effects, as represented by predicted understory variables scaled by $\hat{\beta}_3$ are still changing in accord with the stand history and condition.

The final parameter estimates for the full model are shown in Table 4. Note that these statistical tests are approximate because the model itself was constrained to have the parameter estimates values for β_3 and β_4 as explained above. The bias (computed using residuals as observed minus predicted) and the root mean squared error are also shown in the same table.

Here we show the model to clarify its use. The proposed height growth model predicts tree height at the end of a period (i.e., time 1, t_1), "h_1", as

$$h_{1_{(i,j)}} = \hat{a}_j\{1 - [1 - (h_{0_{(i,j)}}/\hat{a}_j)] \exp[-b'(t_1 - t_0)]\}^{1/0.73708},$$

$$b' = 0.02018\left[1.29031 - \frac{1}{1 + e^{\theta}}\right],$$

$$\theta = 0.06149 + 0.04677\,\mathrm{BAL}_{0_{(i,j)}} - 0.36722\,\frac{\mathrm{BAL}_{0_{(i,j)}}}{\sqrt{h_{0_{(i,j)}}}} + \left(\frac{\mathrm{UH}_{0_{(j)}}}{h^2_{0_{(i,j)}}}\right) \cdot (-0.09243\,\mathrm{UCOVER}_{0_{(j)}}), \quad (10)$$

where $h_{1_{(i,j)}}$ is height at the end of the period for the ith tree at the jth plot (in m), $\hat{a}_j$ is the predicted asymptote at the jth plot (in m) using the site-factor model (Table 3), $h_{0_{(i,j)}}$ is height at the beginning of the period for the ith tree at the jth plot (in m), $t_1 - t_0$ is the period of prediction, $\mathrm{BAL}_{0_{(i,j)}}$ is basal area in trees larger than the ith tree at the jth plot at the beginning of the period (in m^2/ha), $\mathrm{UH}_{0_{(i,j)}}$ is understory height at the jth plot at the beginning of the period (in m), and $\mathrm{UCOVER}_{0_{(i,j)}}$ is understory cover at the jth plot at the beginning of the period (in %).

Diagnostic graphs of the standardized residuals showed no concerns for the model assumptions (Figure 2). Based on the median of the predictions for the smallest height class, the model seems to be biased; however, the data are positively skewed, so the mean will be higher than the median and therefore the bias will be less than it appears. As a matter of fact, the small trees have a smaller bias than the overall average, 0.39% versus 0.51%. The root mean squared error of the model is 4.56%.

Table 4. Parameter estimates for the proposed height growth model

Parameter	Estimate	SE	t value	P value
β_0	0.06149	0.0316	1.9450	0.0519
β_1	0.04677	0.0066	7.0686	<0.00001
β_2	−0.36722	0.0284	−12.9340	<0.00001
β_3	−0.09243	0.0092	−10.0458	<0.00001
β_4	1.29031	0.0261	49.4381	<0.00001

Note that the parameters β_0, β_1, and β_2 were estimated using the entire data set, whereas β_3 and β_4 were estimated using the data sets with which understory variables were measured. The P-values are approximate because the nature of the fitting approach used. Fit statistics: root mean squared error = ±0.8977 m; bias = 0.0890 m.

Behavior Analysis

Height Growth under Different Levels of Stand Basal Area

We numerically computed the instantaneous height growth [i.e., derivative (dh/dt)] using the proposed model (Table 4). This derivative corresponds to the height increment in 1 year. It must be pointed out that even though a discrete time step differential equation is being solved, the finite difference for 1 year corresponds to the derivative in this case, because the height increment for a period less than 1 year (how the growth rate changes within a season) is well beyond the scope of this project and model. The derivative of the model was computed using four different basal area in larger trees levels (5, 10, 20, and 40 m^2/ha) as constant through time (up to year 150). We assumed for this computation the following values for the other needed variables: an average understory height (UH) of 1 m and understory cover (UCOVER) of 20%. The initial conditions were $h_0 = 0.2$ m and $t_0 = 5$ years, and an asymptote of 45 m was assumed. Figure 3a summarizes this framework in a system dynamics diagram. The plots of the current annual height increments against time and height are shown in Figure 4.

Dynamic System

Several authors have pointed out the importance of modeling complex systems (e.g., a forest) as an interacting dynamic system, both in the forestry literature (Leary 1970, García 1994, Stage 2003) and in the literature on general biological problems (Haefner 1996, Adler 1998). In dynamic systems, the main idea is to characterize the state of the system at any point in time so that given the present state the future does not depend on the past (García 1994); this may be called the state-space approach (Aoki 1990, García 1994, Buckland et al. 2004).

Even though building such a dynamic system is beyond the scope of this study, we could predict the development of the auxiliary variables (i.e., basal area in larger trees, understory cover, and understory height) of our height growth model using Prognosis (Stage 1973, Wykoff et al. 1982) and then review the behavior of this model. For this purpose, we have implemented a simple continuous-time dynamic system model (Adler 1998), as follows, to assess the behavior of the proposed model.

We used the proposed height growth model. Based on this expression, we can express the rate of change of the state variable, height, as a function of the state variable itself. As forests are dynamic systems, we should also represent the other stand variables in differential equation form. Because of the major effect of stand basal area in forest management practices we developed a differential equation model for this variable from the yield tables of Stage et al. (1988) for a naturally regenerated stand on a site index of 21.3 m (70 ft) in the same region (Inland Northwest). Using those values, we fitted a growth model (Equation 2, where now instead of modeling h_1 we are modeling stand basal area at time 1, G_1) using nonlinear regression and find the parameter estimates for *a, b,* and *c* for the basal

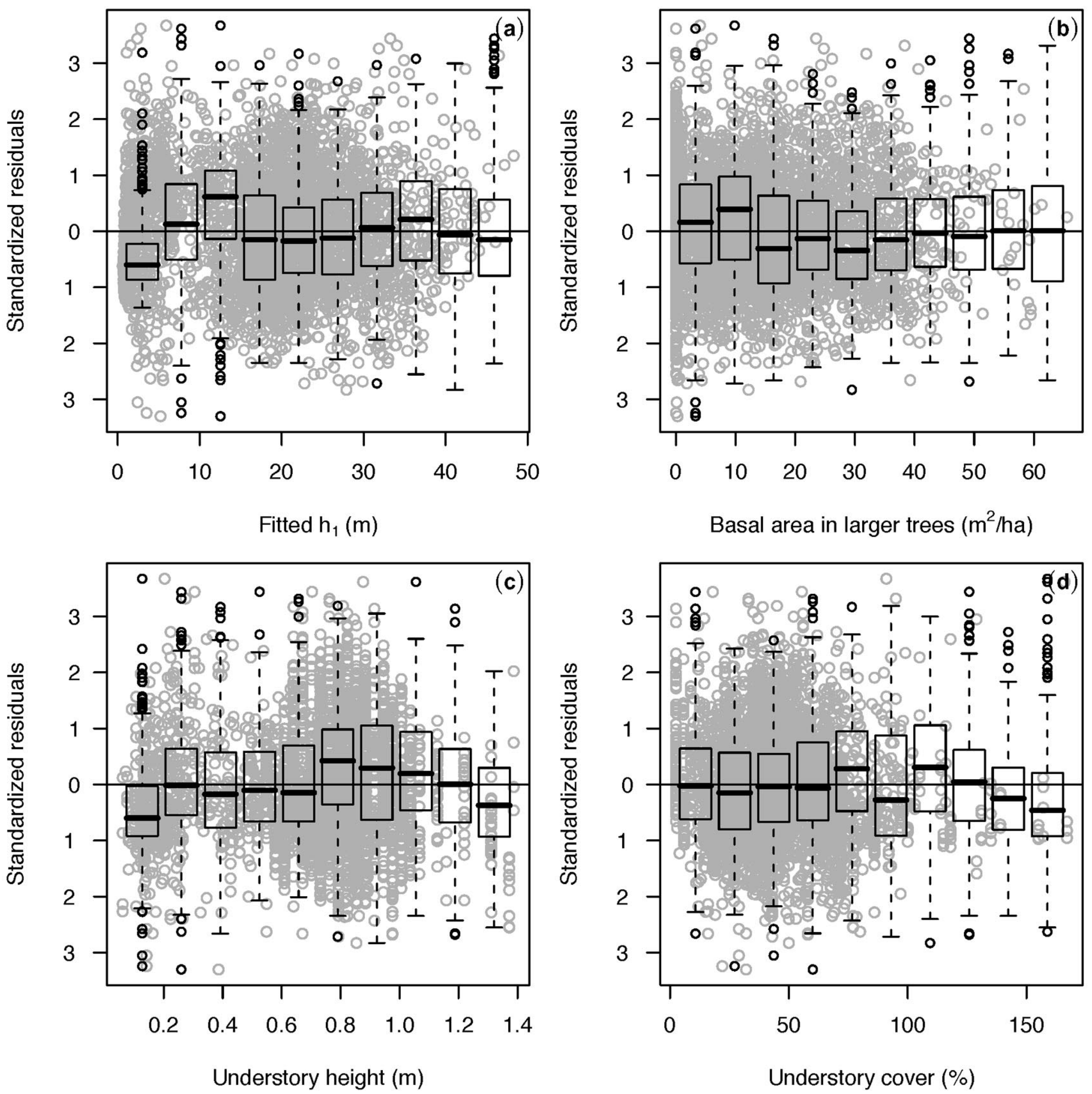

Figure 2. Standardized residuals of the proposed model against predicted values (a), basal area in larger trees (b), understory height (c), and understory cover (d). Boxplots of the standardized residuals by 10 classes (defined by the percentiles, therefore drawn using the same numbers of observations) of each variable.

area yield function. The equation for stand basal area (in metric units) in a Douglas-fir naturally regenerated stand is

$$G_1 = 61.6171\{1 - [1 - (G_0/61.6171)^{0.22812}] \exp[-0.03479(t_1 - t_0)]\}^{1/0.22812}. \quad (11)$$

Based on the above, we built the following dynamic systems, from a simpler one to a more realistic one:

a. Height growth and basal area in larger trees interacting simultaneously. We simulate a system, in which height and basal area in larger trees are interacting simultaneously (Figure 3b). Using Equation 11 and, as our model uses BAL, we used four different percentages (0, 30, 60, and 90%) of the stand basal area trajectories, as values for BAL. These trajectories of BAL might be interpreted as an approximation to the crown class of trees. UH and UCOVER variables were set to be constant through time (in the absence of suitable differential equations), with values of 1 m and 20%, respectively. The initial conditions were h_0 = 0.2 m, t_0 = 5 years, and BAL_0 = 0.23 m²/ha. We assume a fixed value for the asymptote of 45 m (we also could have used the site variable model). Finally, we plot the height yield depending on the levels of BAL running simultaneously with our height growth model.

b. Height growth, basal area in larger trees, and understory height interacting simultaneously. We did not have data for fitting a model for understory height, but we instead built an equation that allowed us to simulate the fact that understory height would be greater than tree height until tree height reaches some threshold height (we use 1.3 m). The model is a function of tree height as follows

$$\mathrm{UH} = k_1\left(\frac{1 - e^{-k_2(k_1 h)}}{1 - e^{-k_2}}\right), \quad (12)$$

where UH is understory height, h is tree height, and k_1 and k_2 are parameters that set to be equal to 1.3 and 0.3, respectively.

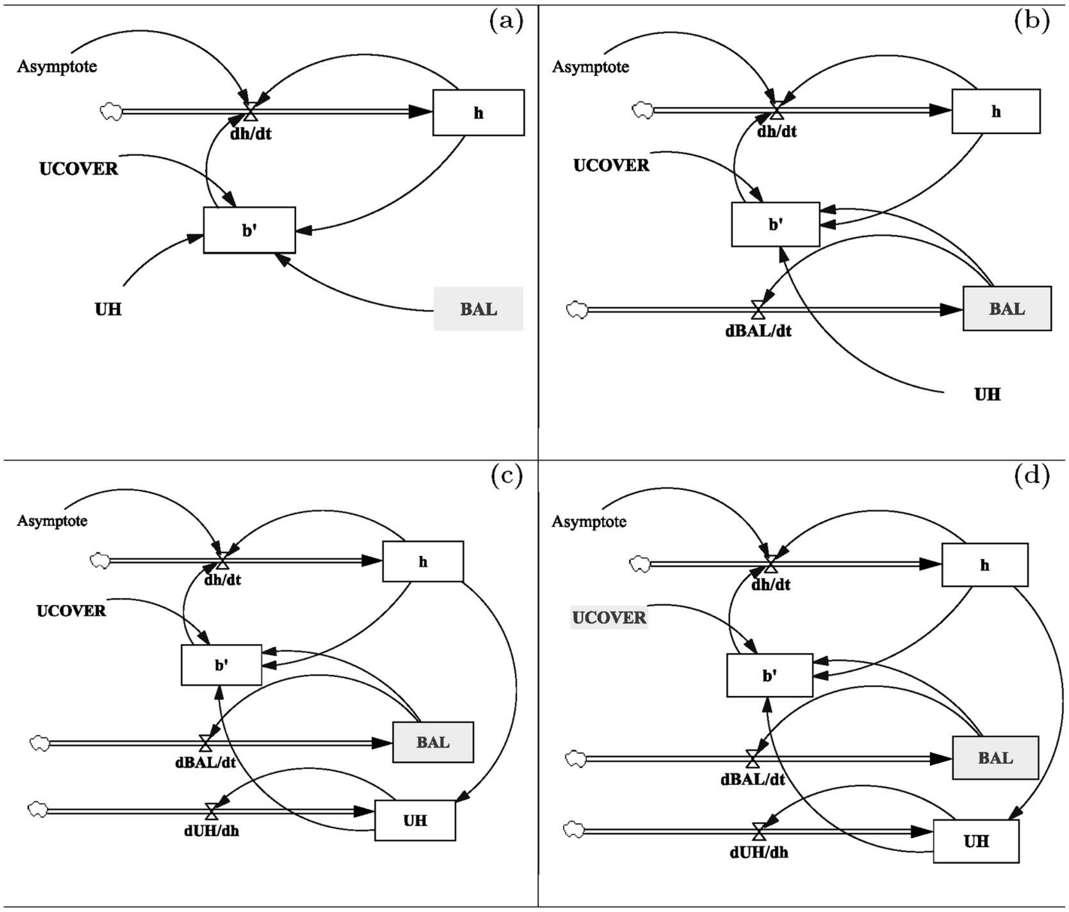

Figure 3. Dynamic system diagrams. State variables are represented by boxes, derivatives by tick arrows with control valves (*rates*, *flows*), and the dependence of rate on state variables by curved arrows. All the rest are constants. A variable (or constant) in a gray box means that some levels of it were used. b' is representing expression 4. The systems are the following: system having only the height growth model as the differential equation and constant levels of BAL (a); system having differential equations for both height growth and BAL with different trajectories of BAL (b); system also having a differential equation for understory height (c); and system as previously but using different constant levels of understory cover (d).

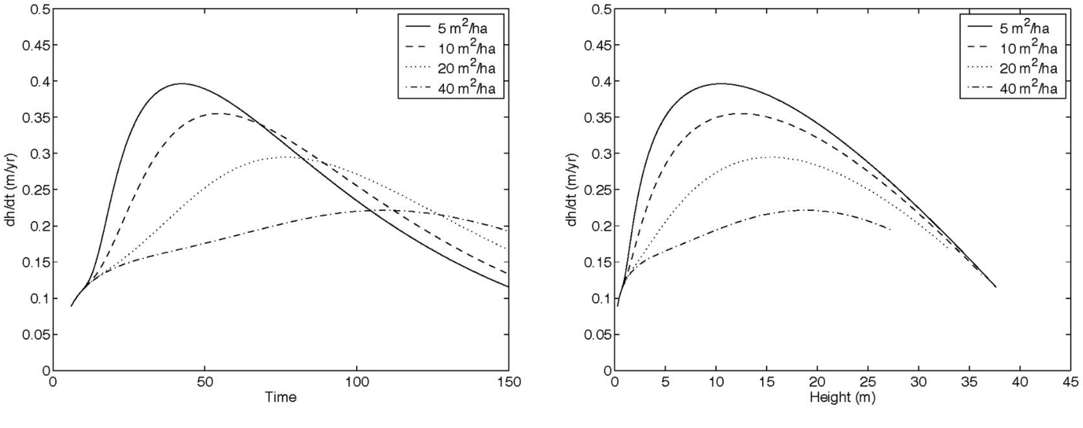

Figure 4. Height growth against time (left) and height (right), for constant basal areas in larger trees of 5, 10, 20, and 40 m^2/ha. An asymptote of 45 m was used for this figure.

Then we included the understory height function (Equation 12) in our previous system, allowing the same levels for the rest of variables as explained above. This analysis allows us to examine the effect of understory height for very small trees for different crown classes (i.e., different BAL trajectories) of trees. Figure 3c summarizes this framework in a system dynamics diagram.

c. Height growth, basal area in larger trees, and understory height interacting simultaneously for different levels of understory cover. So far, we only tested having one value of UCOVER, but here we allow different levels of understory cover to test its effect in the behavior of the model (Figure 3d). We use four levels of understory cover (0, 40, 100, and 160%).

Dynamic Analyses of the Fitted Model

The model not only shows different levels of maximum height growth (derivative plots, Figure 4) but also different times when this occurs, which is a desirable property. It is important to point out that these plots (Figure 4) only show the potential behavior of height growth using our models but are not accounting for the fact that a Douglas-fir tree under heavy suppression for more than 140 years would not survive such suppression.

We assumed different constant values for basal area in larger trees as a percentage of the stand basal and simulate the height, representing the system of Figure 3a. Also, we used a differential equation (Equation 11) for representing four different trajectories of basal area in larger trees and simulate height, representing the system of Figure 3b. Heights for both systems are shown in Figure 5. Even though similar, the curves of this figure show that when considering understory height as a function that varies according to the tree height, the model produces a reduction of height as expected, and this reduction is more pronounced for trees with greater values of basal area in larger trees (i.e., intermediate and suppressed trees). In Figure 6 instead of only using a constant value for understory cover, we used two values to represent two different competing vegetation scenarios.

A full system for which we have differential equations for tree height, BAL, and UH under different levels of understory cover was also simulated, as depicted in Figure 3d. We represent this system for the most dominant tree in the stand, that is, the tree with BAL = 0, and for an intermediate tree, with BAL = 60% of the stand basal area. Height yields for both types of trees are shown in Figure 7.

Discussion

The random effects are representing the hierarchical structure, which recognizes correlation among estimates for individual trees within each plot. To use more than one random parameter, however, produces strong correlation among random-effects estimates of the parameters *a* and *b*. As Pinheiro and Bates (2000) pointed out, this situation can result in an ill-conditioned estimated variance-covariance matrix, which suggests that the random-effects structure may be overparameterized. Similar behavior of an overparameterized model was found by Gregoire and Schabenberger (1996) in volume equations, as well as by Hall and Bailey (2001) in a height growth model using the Richards function.

It is important to point out that the asymptote that we are using here (45 m) for simulating the behavior of the model is not a site index. Site index is the dominant height at base-age 50 for Douglas-fir, and the asymptote is height at infinite age. For comparison purposes we can compare the height of our model for a dominant tree (the left panel of Figure 7) with the height predicted by using Monserud's (1984) site index equation (the use of this model in prediction is more clearly explained in Monserud 1985) for a site-index of 21.3 m (70 ft) (as used in the present article when fitting the stand basal area model, see Eq. 11). Our model predicts 20.7 m. This result shows that our model produces reasonable predictions for dominant trees, even though it includes density effects. Furthermore, the asymptote of 45 m that we are using in our behavior analysis is similar to that determined using Monserud's (1984) equation for a tree growing in a Douglas-fir habitat type series.

Simulation of dynamic systems that involve proposed model(s) are fundamental in growth modeling. Following the normal practice in statistics, we first analyze the "pure" effect of each variable in the model. That is to say, we only modify one variable and keep the remaining constant (as showed in Figure 4, when we were varying BAL), and see the behavior of the model. Nevertheless, use of this procedure for testing the effect of competing vegetation variables did not show much effect when in fact there is (as shown in Figure 6). Therefore, dynamic systems are not only important for growth modeling in ecology but also offer utility for testing statistical models. As shown in the present research, even though we lack sufficient data for building models for

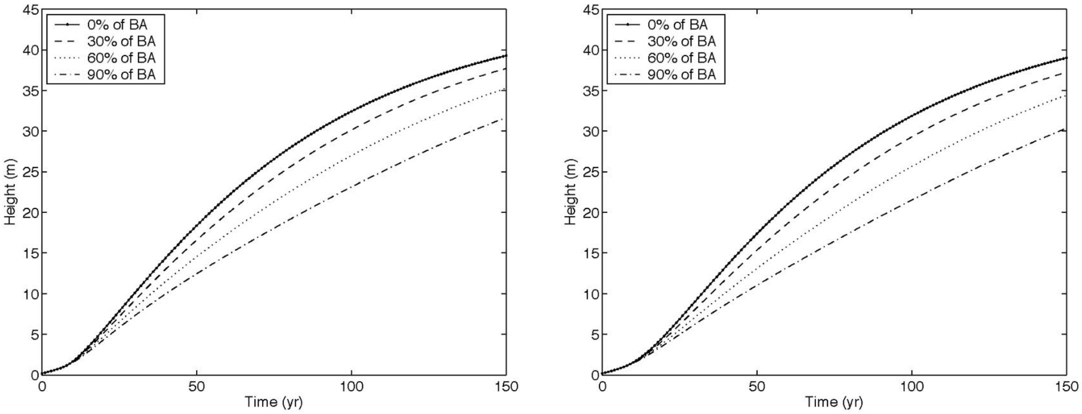

Figure 5. Height development for different levels of basal area in larger trees, expressed as a percentage of the stand basal area using a constant value (left) and a differential equation for understory height (right). Note that basal area in larger trees of 0% of the stand basal area identifies the most dominant tree in a stand, and 90% identifies one of the most suppressed trees in a stand.

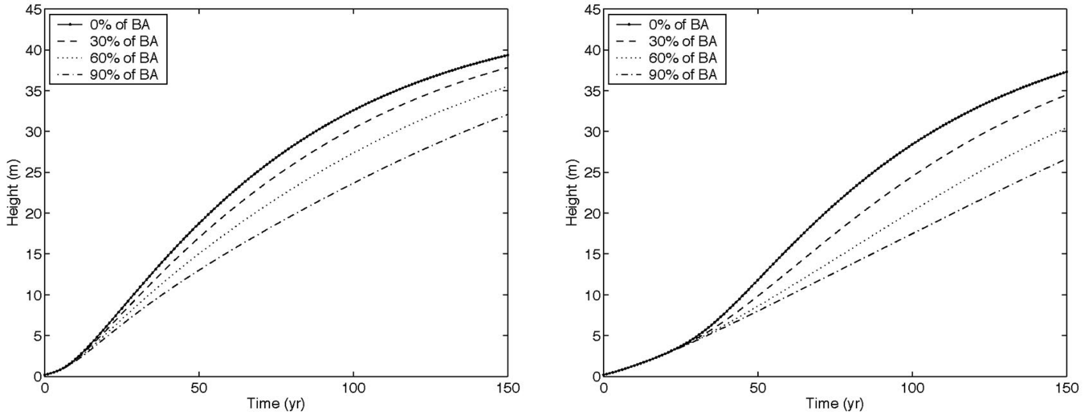

Figure 6. Height development for different levels of basal area in larger trees and a differential equation for understory height when the tree is growing under understory cover of 10% (left) and 100% (right). Note that basal area in larger trees of 0% of the stand basal area identifies the most dominant tree in a stand, and 90% identifies one of the most suppressed trees in a stand.

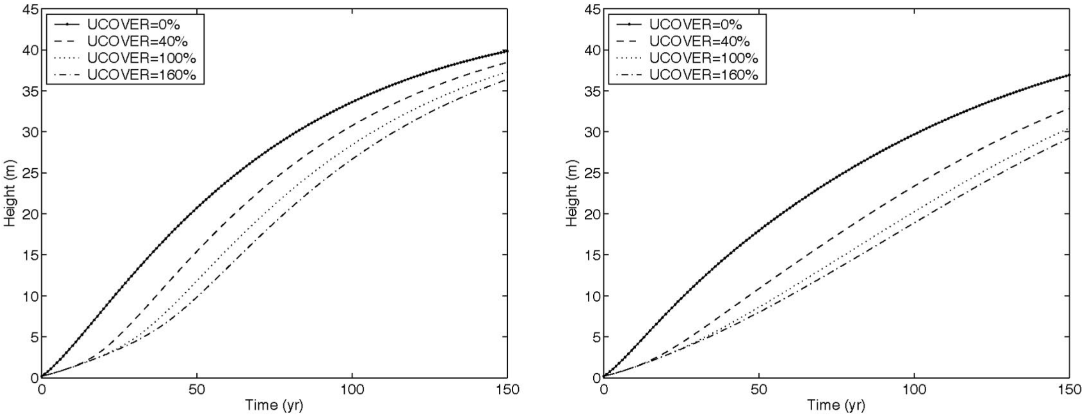

Figure 7. Height development for different simultaneous levels of basal area in larger trees and under interacting understory height, using different constant levels of understory cover for a dominant tree (left) and for an intermediate tree (right).

all of the variables that should be included in the system, mathematical models with assumed parameters that behave according to the literature offer us a way to overcome the lack of data for those variables and allow us to more realistically evaluate the behavior of the model.

The left panel of Figure 7 shows growth patterns for a dominant tree—the one that would be used in calculating site index. Even with the modest effects of understory competition (40%) represented in these data, ignoring early competition would seriously bias site index (20.7 m versus 15.4 m).

Therefore, use of site variables as measures of site productivity has the following two advantages: first, these variables are in a space of different units of measure than site index, which has the same dimension as the height growth model. Being able to omit site index as a predictor variable in height growth models also helps to achieve the independence assumption among variables used in statistical models. Second, these variables are not affected by stand density and stand structure. Therefore, with this approach we can use a broader concept of site productivity.

Further analysis should be focused on simultaneously fitting a system of differential equations for each variable included in our model. Equations that are part of a simulation model share variables and parameters (e.g., the height growth model and the basal area equation), and fitting the equations for these variables one at a time may not be satisfactory (García 1988) and may result in biological monstrosities (Stage 2003). This multiresponse nature of forest growth models can be overcome by simultaneously fitting a system of equations. Some applications of this concept have been included by García (1984) in New Zealand, Monserud et al. (1997) in Austria, and García and Ruiz (2003) in Spain. Another approach is to fit multivariate mixed-effects models (Hall and Clutter 2004). Furthermore, a simultaneous fit of equations might decrease the number of variables (and parameters) of our height growth model, based on the findings of Hasenauer et al. (1998), facilitating the fitting process too. Notice, however that simultaneous fit is possible when one has data with simultaneous measurements too. An important objective of this article was to build a comprehensive model with less-than-comprehensive data.

The proposed model behaves according to the literature that has been reported for competing vegetation effects (i.e., controlling competing vegetation would increase the yield of a stand). The use of BAL allows us to model height growth of all crown class trees and not just dominant trees, as when using site index models.

Concluding Remarks

Density is an important variable to model height growth. Modifying the original parameters of a differential linear equation with power transformation to include competition effects from understory and overstory improves the fit compared with the model without density effects.

Our results have shown that there is a density effect on height growth of trees of all dominance classes and that more accurate height growth predictions can be obtained by considering density. Therefore, the usual approach of predicting height growth through site index curves for Douglas-fir in the Inland Northwest should be reconsidered.

Further analysis should be conducted to use other variables (instead of site index) to predict site productivity of Douglas-fir. We show that use of site factors, such as elevation, slope, aspect, and forest habitat type, produces a good fit for estimating the asymptote. Our model uses an integrated form of a differential equation with the following properties: it does not depend on age, it uses data that have different measurement period lengths, it can predict height for different period lengths, site productivity is represented by factors other than height growth because competition affects height growth, and with only one model we can make predictions for both juvenile and older trees (no discontinuities).

Endnote

[1] We also tested inclusion of the number of small trees (conifers) in our model, to represent the competition coming from small trees. However, we did not find any significant improvement in the model. We speculate that no improvement was found because with the INGY experiment, even though the correlation between good sites and greater understory was reduced, it still was a problem for small conifers because they were not thinned.

Literature Cited

ADLER, F.R. 1998. *Modeling the dynamics of life: Calculus and probability for life scientists.* Brooks/Cole Publishing Co., New York, NY. 784 p.

AKAIKE, H. 1973. Information theory and an extension of the maximum likelihood principle. P. 267–281, in *Second International Symposium on Information Theory,* Petrov, B.N., and G. Czaki (eds.). Akademiai Kiadó, Budapest, Hungary.

ALEXANDER, R.R. 1966. *Site indexes for lodgepole pine, with corrections for stand density: Instructions for field use.* US For. Serv. Res. Paper RM-24. 7 p.

ALEXANDER, R.R., D. TACKLE, AND W.G. DAHMS. 1967. *Site indexes for lodgepole pine, with corrections for stand density: Methodology.* US For. Serv. Res. Paper RM-29. 18 p.

AOKI, M. 1990. *State space modeling of time series*. 2nd ed. Springer-Verlag, New York, NY. 323 p.

ASSMANN, E. 1970. *The principles of forest yield study.* English ed. Pergamon Press, Oxford, England. 506 p.

BUCKLAND, S.T., K.B. NEWMAN, L. THOMAS, AND N.B. KOESTERS. 2004. State-space models for the dynamics of wild animal populations. *Ecol. Model.* 171(1–2):157–175.

CAO, Q.V. 2004. Annual tree growth predictions from periodic measurements. P. 212–215, in *Proc. of the 12th Biennial Southern Silvicultural Research Conference*, Connor, K. F. (ed.). US For. Serv. Gen. Tech. Rep. SRS-71. Asheville, NC.

CIESZEWSKI, C.J., AND I.E. BELLA. 1993. Modeling density-related lodgepole pine height growth, using Czarnowski's stand dynamics theory. *Can. J. For. Res.* 23(12):2499–2506.

CLUTTER, J.L., J.C. FORTSON, L.V. PIENAAR, G.H. BRISTER, AND R.L. BAILEY. 1983. *Timber management: A quantitative approach.* Wiley, New York, NY. 333 p.

DANIEL, T.W., J.A. HELMS, AND F.S. BAKER. 1979. *Principles of silviculture.* 2nd ed. McGraw-Hill, New York, NY. 521 p.

DENNIS B, J.M. PONCIANO, S.R. LELE, M.L. TAPER, AND D. STAPLES. 2006. Estimating density dependence, process noise and observation error. *Ecol. Monogr.* 76(3):323–341.

FERGUSON, D.E., A.R. STAGE, AND R.J. BOYD. 1986. Predicting regeneration in the grand fir-cedar-hemlock ecosystem of the Northern Rocky Mountains. *For. Sci. Monogr.* 26:41 p.

FLEWELLING, J., R. COLLIER, R. GONYEA, D. MARSHALL, AND E. TURNBLOM. 2001. Height-age curves for planted stands of Douglas-fir, with adjustments for density. SMC Working Paper 1, College of Forest Resources, Univ. of Washington, Seattle, WA. 25 p.

FRANKLIN, P. 1944. *Methods of advanced calculus*. McGraw-Hill Book Company, New York, NY. 486 p.

GAISER, R.N., AND R.W. MERZ. 1951. Stand density as a factor in estimating white oak site index. *J. For.* 49(8):572–574.

GARCÍA, O. 1979. Modelling stand development with stochastic differential equations. P. 315–333, in *Mensuration for management planning of exotic forest plantations*, Elliott, D.A. (ed.). FRI Symposium No. 20. Forest Research Institute, New Zealand Forest Service, Rotorua, NZ.

GARCÍA, O. 1983. A stochastic differential equation model for the height growth of forest stands. *Biometrics* 39(4):1059–1072.

GARCÍA, O. 1984. New class of growth models for even-aged stands: *Pinus radiata* in Golden Downs forest. *N.Z. J. For. Sci.* 14(1):65–88.

GARCÍA, O. 1988. Growth modelling—A (re)view. *N.Z. For.* 33(3):14–17.

GARCÍA, O. 1994. The state-space approach in growth modelling. *Can. J. For. Res.* 24:1894–1903.

GARCÍA, O. 2005. Comparing and combining stem analysis and permanent sample plot data in site index models. *For. Sci.* 51(4):277–283.

GARCÍA, O., AND F. RUIZ. 2003. A growth model for eucalypt in Galicia, Spain. *For. Ecol. Manag.* 173(1–3):49–62.

GARRISON, M.T., P.G. MIKA, T.M. SHAW, AND J.A. MOORE. 1997a. Six year response to N and K fertilization for Douglas-fir in south-central Washington (Klickitat). Tech. Rep. Intermountain Forest Tree Nutrition Cooperative, Univ. of Idaho, Moscow, ID. 14 p.

GARRISON, M.T., J.A. MOORE, T.M. SHAW, AND P.G. MIKA. 2000. Foliar nutrient and tree growth response of mixed-conifer stands to three fertilization treatments in northeast Oregon and north central Washington. *For. Ecol. Manag.* 132(4):183–198.

GARRISON, M.T., T.M. SHAW, J.A. MOORE, AND P.G. MIKA. 1997b. Forest health and nutrition study: Establishment report. Tech. Rep. Intermountain Forest Tree Nutrition Cooperative, Univ. of Idaho, Moscow, ID. 9 p.

GOLSER, M., AND H. HASENAUER. 1997. Predicting juvenile tree height growth in uneven-aged mixed species stands in Austria. *For. Ecol. Manag.* 97(4):133–146.

GREGOIRE, T.G., AND O. SCHABENBERGER. 1996. A non-linear mixed-effects model to predict cumulative bole volume of standing trees. *J. Appl. Stat.* 23(2/3):257–271.

HAEFNER, J.W. 1996. *Modeling biological systems: Principles and applications*. Chapman & Hall, New York, NY. 473 p.

Hall, D.B., and R.L. Bailey. 2001. Modeling and prediction of forest growth variables based on multilevel nonlinear mixed models for timber yield predictions. *For. Sci.* 47(3):311–321.

Hall, D.B., and M. Clutter. 2004. Multivariate multilevel nonlinear mixed effects models for timber yield predictions. *Biometrics* 60(3):16–24.

Hann, D.W., and M.W. Ritchie. 1988. Height growth rate of Douglas-fir trees: A comparison of model forms. *For. Sci.* 34(1):165–175.

Harville, D.A. 1977. Maximum likelihood approaches to variance component estimation and to related problems. *J. Am. Stat. Assoc.* 72(358):320–338.

Hasenauer, H., R.A. Monserud, and T.G. Gregoire. 1998. Using simultaneous regression techniques with individual-tree growth models. *For. Sci.* 44(1):87–95.

Hessburg, P.F., and J.K. Agee. 2003. An environmental narrative of Inland Northwest United States forests, 1800–2000. *For. Ecol. Manag.* 178(2):23–59.

Husch, B., T.W. Beers, and J.A. Kershaw. 2003. *Forest mensuration*. 4th ed. Wiley, New York, NY. 443 p.

INGY. 1999. Small tree/competing vegetation study, installation and data collection procedures. P. 98–129, in *Annual report to steering committee for calendar year 1998*, Milner, K. (ed.). Inland Northwest Growth and Yield Cooperative, University of Montana, Missoula, MT.

Kerr, G. 2003. Effects of spacing on the early growth of planted *Fraxinus excelsior* L. *Can. J. For. Res.* 33(7):1196–1207.

Krajicek, J.E., K.A. Brinkman, and S.F. Gingrich. 1961. Crown competition factor—A measure of density. *For. Sci.* 7(1):35–42.

Laird, N.M., and J.H. Ware. 1982. Random-effects models for longitudinal data. *Biometrics* 38(4):963–974.

Leary, R.A. 1970. *System identification principles in studies of forest dynamics.* US For. Serv. Res. Paper NC-45. 38 p.

Lloyd, F.T., and E.P. Jones, Jr. 1983. Density effects on height growth and its implications for site index prediction and growth projection. P. 329–333, in *Proc. of the Second Biennial Southern Silvicultural Research Conference*, Jones, E.P. Jr. (ed.). US For. Serv. Gen. Tech. Rep. SE-24. Asheville, NC.

Loveall, M.W. 2000. *A height growth model for young lodgepole pine in Western Montana: Quantifying small tree and competing vegetation relationships*. M.Sc. thesis, Univ. of Montana, Missoula, MT. 49 p.

MacFarlane, D.W., E.J. Green, and H.E. Burkhart. 2000. Population density influences assessment and application of site index. *Can. J. For. Res.* 30(9):1472–1475.

MacLean, C.D., and C.T. Scott. 1987. Interpolating current annual growth from two dbh measurements. P. 1118–1123, in *Forest Growth Modelling and Prediction*, *Vol. 2. Proc. IUFRO Conference,* Ek, A.R., S.R. Shifley, and T.E. Burk (eds.), US For. Serv. Gen. Tech. Rep. NC-120. Minneapolis, MN.

Mason, E.G. 2001. A model of the juvenile growth and survival of *Pinus radiata* D. *Don. New For.* 22(1–2):133–158.

Mason, E.G., D.B. South, and Z. Weizhong. 1996. Performance of *Pinus radiata* in relation to seedling grade, weed control, and soil cultivation in the central North Island of New Zealand. *N.Z. J. For. Sci.* 26(1/2):173–183.

McCulloch, C.E., and S.R. Searle. 2001. *Generalized, linear, and mixed models.* Wiley-Interscience, New York, NY. 325 p.

Monserud, R.A. 1984. Height growth and site index curves for Inland Douglas-fir based on stem analysis data and forest habitat type. *For. Sci.* 30(4):943–965.

Monserud, R.A. 1985. *Applying height growth and site index curves for Inland Douglas-fir.* US For. Serv. Res. Paper INT-347. 22 p.

Monserud, R.A., H. Sterba, and H. Hasenauer. 1997. The single-tree stand growth simulator PROGNAUS. P. 50–56, in *Proc. of Forest Vegetation Simulator Conference,* Teck, R., M. Mouer, and J. Adams (eds.). US For. Serv. Gen. Tech. Rep. INT-373. Ogden, UT.

Moore, J.A., and P.G. Mika. 1997. Influence of soil parent material on the nutrition and health of established conifer stands in the Inland Northwest. P. 112–117, in *Symposium: forest seedling nutrition from the nursery to the field,* Haase, D.L., and R. Rose (eds.). Nursery Technology Cooperative, Dept. of For. Sci., Oregon State University, Corvallis, OR.

Moore, J.A., P.G. Mika, and J.L. Vander Ploeg. 1991. Nitrogen fertilizer response of rocky mountain Douglas-fir by geographic area across the Inland Northwest. *West. J. Appl. For.* 6(2–3):94–98.

Mouer, M. 1985. *COVER: A user's guide to the CANOPY and SHRUBS extension of the stand Prognosis model.* US For. Serv. Gen. Tech. Rep. INT-190. 49 p.

Nigh, G.D., and B.A. Love. 1999. A model for estimating juvenile height of lodgepole pine. *For. Ecol. Manag.* 123(2): 157–166.

Ochi, N., and Q.V. Cao. 2003. A comparison of compatible and annual growth models. *For. Sci.* 49(2):285–290.

O'Hara, K.L., P.A. Latham, P. Hessburg, and B.G. Smith. 1996. A structural classification for Inland Northwest forest vegetation. *West. J. Appl. For.* 11(3):97–102.

Pienaar, L.V., and B.D. Shiver. 1984. An analysis and models of basal area growth in 45-year-old unthinned and thinned slash pine plantation plots. *For. Sci.* 30(4):933–942.

Pienaar, L.V., and K.J. Turnbull. 1973. The Chapman-Richards generalization of von Bertalanffy's growth model for basal area growth and yield in even-aged stands. *For. Sci.* 19(1):2–22.

Pinheiro, J.C., and D.M. Bates. 2000. *Mixed-effects models in S and Splus.* Springer-Verlag, New York, NY. 528 p.

R Development Core Team. 2006. *R: A language and environment for statistical computing* [version 2.4.1]. R Foundation for Statistical Computing, Vienna, Austria. Available online at www.r-project.org; last accessed Dec. 20, 2006.

Rennolls, K. 1995. Forest height growth modelling. *For. Ecol. Manag.* 71(3):217–225.

Richards, F.J. 1959. A flexible growth function for empirical use. *J. Exp. Bot.* 10(29):290–300.

Salas, C. 2006. *Modelling effects of overstory density and competing vegetation on tree height growth.* M.Sc. thesis, Univ. of Idaho, Moscow, ID. 58 p.

Salas, C., A.P. Robinson, and A.R. Stage. 2005. Developing a biological height growth model incorporating competition effects. In *Integrating Inventory, Growth Modelling, and Forest Planning*, Inland Northwest Growth and Yield Cooperative (INGY) annual winter technical meeting, Jan. 18, 2005, Spokane, WA.

Schabenberger, O., and F.J. Pierce. 2002. *Contemporary statistical models for the plant and soil sciences.* CRC Press, Boca Raton, FL. 738 p.

Scott, W., R. Meade, R. Leon, D. Hyink, and R. Miller. 1998. Planting density and tree-size relations in coast Douglas-fir. *Can. J. For. Res.* 28(1):74–78.

Smith, D.M., B.C. Larson, M.J. Kelty, and P.M.S. Ashton. 1997. *The practice of silviculture: Applied forest ecology.* 9th ed. Wiley, New York, NY. 537 p.

Spurr, S.H. 1952. *Forest inventory.* Ronald Press, New York, NY. 476 p.

Stage, A.R. 1973. *Prognosis model for stand development.* US For. Serv. Res. Paper INT-137. 32 p.

STAGE, A.R. 2003. How forest models are connected to reality: Evaluation criteria for their use in decision support. *Can. J. For. Res.* 33(3):410–421.

STAGE, A.R., AND R.J. BOYD. 1987. Evaluation of growth and yield responses to vegetation management of the mixed-conifer forests in the Inland Northwest. P. 295–324, in *Forest vegetation management for conifer production*, Walstad, J.D., and P.J. Kuch (eds.). Wiley, New York, NY.

STAGE, A.R., D.L. RENNER, AND R.C. CHAPMAN. 1988. *Selected yield tables for plantations and natural stands in Inland Northwest forests.* US For. Serv. Res. Paper INT-394. 58 p.

STAGE, A.R., AND C. SALAS. 2007. Interactions of elevation, aspect and slope in models of forest species composition and productivity. *For. Sci.* 53(4):486–492.

STAPLES, D.F., M.L. TAPER, AND B. DENNIS. 2004. Estimating population trend and process variation for PVA in the presence of sampling error. *Ecology* 85(4):923–929.

UZOH, F.C.C., AND W.W. OLIVER. 2006. Individual tree height increment model for managed even-aged stands of ponderosa pine throughout the western United States using linear mixed effects models. *For. Ecol. Manag*. 221(1/3):147–154.

VALENTINE, H.T. 1997. Height growth, site index, and carbon metabolism. *Silva Fenn.* 31(3):251–263.

VAN LAAR, A., AND A. AKÇA. 1997. *Forest mensuration*. Cuvillier Verlag, Göttingen, Germany. 418 p.

VANCLAY, J.K. 1994. *Modelling forest growth and yield: Applications to mixed tropical forests.* CAB International, Wallingford, Berkshire, England. 312 p.

VON BERTALANFFY, L. 1957. Quantitative laws in metabolism and growth. *Q. Rev. Biol.* 32(3):217–231.

VON GADOW, K., AND G. HUI. 1998. *Modelling forest development*. Cuvillier Verlag, Göttingen, Germany. 211 p.

WALSTAD, J.D., AND P.J. KUCH. 1987. Introduction to forest management. P. 3–14, in *Forest vegetation management for conifer production,* Walstad, J.D., and P.J. Kuch (eds.). Wiley, New York, NY.

WATT, M.S., M.O. KIMBERLEY, B. RICHARDSON, D. WHITEHEAD, AND E. G. MASON. 2004. Testing a juvenile tree growth model sensitive to competition from weeds, using *Pinus radiata* at two contrasting sites in New Zealand. *Can. J. For. Res.* 34(3): 1985–1992.

WESTFALL, J.A., H.E. BURKHART, AND H.L. ALLEN. 2004. Young stand growth modeling for intensively-managed loblolly pine plantations in Southeastern U.S. *For. Sci.* 50(6):823–835.

WOODRUFF, D.R., B.J. BOND, G.A. RITCHIE, AND W. SCOTT. 2002. Effects of stand density on the growth of young Douglas-fir trees. *Can. J. For. Res.* 33(3):420–427.

WYKOFF, W.R., N.L. CROOKSTON, AND A.R. STAGE. 1982. *User's guide to the stand Prognosis model.* US For. Serv. Gen. Tech. Rep. INT-133. 112 p.

ZEDAKER, S.M., H.E. BURKHART, AND A.R. STAGE. 1987. General principles and patterns of conifer growth and yield. P. 203–241, in *Forest vegetation management for conifer production,* Walstad, J.D., and P.J. Kuch (eds.). Wiley, New York, NY.

ZEIDE, B. 1993. Analysis of growth equations. *For. Sci.* 39(3):594–616.