A biologically-consistent stand growth model for loblolly pine in the Piedmont physiographic region, USA

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Abstract

A theory-influenced dynamical stand growth model formulation described well the behavior of thinned and unthinned loblolly pine plantations. A simplification containing few free parameters performed as well as a fully parametrized version. It seems particularly well suited to situations where available data is scarce. The stand model can be interfaced to additional climate, nutrition and carbon cycling modules for studying the effects of a changing environment.

Key words: *Pinus taeda*, state space,, hybrid model, carbon, climate change, forest nutrition

1. Introduction

Reliable growth models are essential for effective long-term planning and decision making. This is specially important in intensively managed forest plantations, where it is necessary to evaluate alternative planting densities, thinning regimes, rotation lengths, and possibly pruning, fertilizing, vegetation control, or genetic improvement. Increasingly, there is interest in predicting responses to climate change, and environmental effects such as carbon sequestering. Empirical models describe and generalize observed stand behavior. They can be accurate and highly successful in fulfilling many of the forest manager's needs (Burkhart, 2008). However, they require extensive long-term experimental data, and extrapolation to unobserved situations can be uncertain. A theory-based model would describe hypothesized behavior by reasoning from first principles. At present, available knowledge about tree and stand development is incomplete, and although very useful in furthering research and qualitative understanding, detailed theoretical models may not be as capable of providing the accurate quantitative predictions needed for decision-making (Mohren and Burkhart, 1994; Fontes et al., 2010; García, 2010). Both approaches are combined in hybrid models. These theory-influenced semi-empirical models attempt to be compatible with observations, while at the same time use theoretical knowledge and hypotheses to improve performance under conditions for which data are scarce (Mohren and Burkhart, 1994).

We have developed a biologically consistent whole-stand growth model using data from the Piedmont area in the southeastern US. The main motivation was twofold: 1) Using an extensive data set to test parsimonious model forms that could be used in data-poor situations elsewhere, and 2) Produce a simple and robust base-line model for loblolly pine that can be more easily extended to model effects of climate and nutrition, and biomass and carbon outputs. Data come from thinning trial plots established in the Piedmont region of the southeastern U.S.A. (Burkhart et al., 1985; Amateis et al., 2001). Although the thinning trial includes both Piedmont and Coastal Plain sites, only the Piedmont data were used here.

The model is similar to that of García (2011b). It uses a state-space approach, modelling the rates of change of four state variables that describe the stand at any point in time: top height, trees per hectare, basal area, and a measure of stand closure. Top height growth and its relationship to site quality are represented by a self-contained site-index sub-model. For a given site, the rate of mortality in trees per hectare is modelled as a function of the number of trees and top height. The growth rate of stem volume or biomass per hectare equals gross increment minus mortality. This mortality is the mortality in number of trees multiplied by the mean size of dying trees. In closed-canopy stands, the gross increment is a function of stand density and top height. In young or recently thinned stands that do not yet fully occupy the site, the increment is reduced by an *occupancy* factor, which is non-linearly related to a "relative closure" variable representing the amount of foliage and fine roots. Finally, the rate of increase in closure in open stands is predicted as a function of current closure and top height. Merchantable volumes or other quantities of interest can be estimated as functions of the current state variables. Candidate equation forms for the components were evaluated graphically and statistically, to find those with the best combination of data fitting statistics and parsimony.

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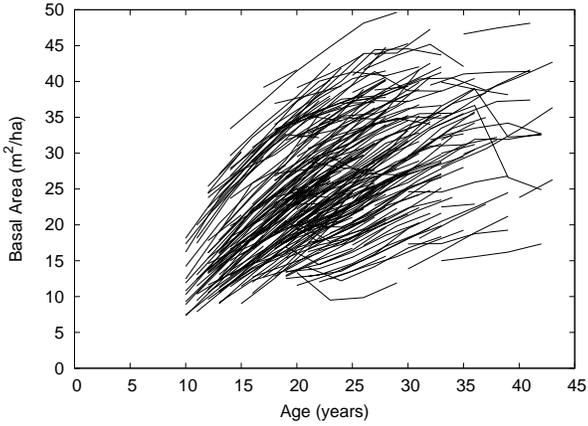
Figure 1: Basal area observations

2. Data

The thinning study was initiated in 1980–1982 throughout the Piedmont and Coastal Plain regions of the southeastern U.S.A. We used the permanent sample plots from the Piedmont physiographic region. Each site had three treatments: unthinned, light thinning, and heavy thinning. Ages at plot establishment varied between 8 and 25 years, with a mean of 15. All diameters at breast height (dbh) and tree heights were measured every three years. Measurements with missing or obviously inconsistent data, or with substantial lightning, pest or other damage were excluded, reducing by 21% the original number of consecutive measurement intervals.

The extent of the data can be seen in Figures 1, 2, and 3. Further details on the experiments are given by Burkhart et al. (1985) and Amateis et al. (2001).

3. Analysis and results

3.1. Height and site

The height of the largest trees in a stand is generally assumed to be largely independent of stand density, at least within certain limits. Its development can then be described by a self-contained sub-model, independently of number of trees or basal area. For this reason, it is also widely used to quantify potential site productivity. In the U.S.A., the most commonly used largest-trees height measure is the mean height of the trees classified as dominant and co-dominant. For loblolly pine, however, increments with this dominant height definition have been found to be sensitive to stand density, and tree selection in low thinnings can cause significant increases in dominant height (Sharma et al., 2002, 2006).

Alternatives include "top height" definitions based on a fixed proportion of largest trees, e.g., the largest 100 per hectare. Because this measure is sensitive to plot size, we defined top height more precisely as the expected height of the largest-dbh tree in a random 0.01 ha plot

(Rennolls, 1978; BC Forest Productivity Council, 1988). This corresponds to approximately the 159 largest trees in one hectare; the interpolated U-estimator of García and Batho (2005) was used to adjust for plot-size. Top height is based on a much smaller proportion of trees than dominant height, and was not appreciably affected by thinnings or stand density. Top height was on average 77 cm larger than the mean of dominants and co-dominants, with a roughly uniform difference at all ages.

The model is a differential form of the Bertalanffy-Richards model,

$$\frac{\mathrm{d}H^c}{\mathrm{d}t} = b(a^c - H^c) \, , \qquad (1)$$

where H is top height (m), t is time in years, and a, b and c are parameters. Estimation followed the method of García (1983). Parametrizations with a and/or b being various functions of a site-dependent parameter q were tested. Best results were obtained with $a = 39.40$, $c = 1.079$, and $b = q$ site-dependent, with $H = 0$ at age 0.

The projection equation (or transition function), estimating a height H_2 at time t_2 given H_1 at t_1, is

$$H_2 = 39.40\{1 - [1 - (H_1/39.40)^{1.079}] \\ \exp[-q(t_2 - t_1)]\}^{1/1.079} \, . \quad (2)$$

In computations it may be more convenient to work with the "invariant"

$$[1 - (H/39.40)^{1.079}]\mathrm{e}^{qt} = \text{constant} \, , \qquad (3)$$

a quantity that remains unchanged in the absence of disturbances.

The conventional site index is related to q by substituting the origin $(t_1, H_1) = (0, 0)$ and the base age 25 years into (2):

$$\text{Site Index} = 39.40(1 - \mathrm{e}^{-25q})^{1/1.079} \, .$$

The data and site-index curves are shown in Figure 2. The site-index curves agree closely with those of McDill and Amateis (1992) and Amateis et al. (2001). Differences from those of Diéguez-Aranda et al. (2006), derived from the pooled Piedmont and Coastal Plain data sets, are small within the range of the data, although larger when extrapolating. The present model is simpler and more convenient. Also, growth depends explicitly on site quality, represented by the parameter q in equations (1) and (2) (García, 2011a).

3.2. Mortality

Natural mortality or survival is extremely variable, and notoriously difficult to predict. A simple but flexible model was used:

$$\frac{\mathrm{d}N}{\mathrm{d}H} = -a_1 H^{a_2} N^{a_3} \, ,$$

where N is number of trees per hectare, and the a_i are parameters (García, 2009). This is similar to models used
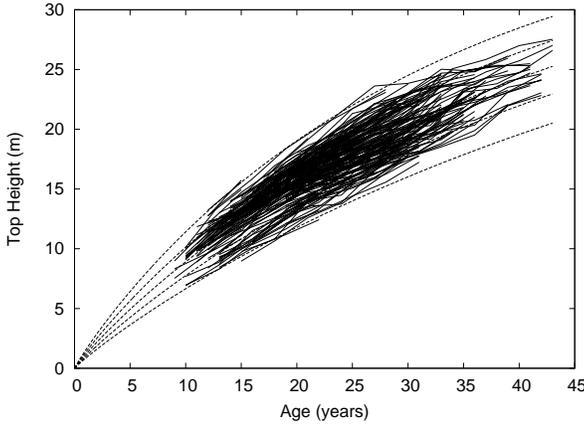
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Figure 2: Top height growth data and model site-index curves. Site indices 14, 16, 18, 20, 22 (base age 25).

Figure 3: Mortality data and model. Projections for initial spacings of 2, 3, . . . , 6 m (top to bottom). Logarithmic y-axis.

by Clutter and Jones (1980) and others (Zhao et al., 2007), but substituting top height for age. Although because of the high correlation between height and age this makes little difference in practice, size may be biologically more significant than chronological age as a causal variable, a principle applied also in equation (1): "The age of a tree and its size tend to increase together. Disentangling the effects of these two factors on tree vitality is no easy task, but further evidence adds to the view that it is size that matters" (Peñuelas, 2005). See also Meinzer et al. (2011).

Also for biological reasons, predictors like basal area or mean diameter have been avoided, considering that the amount of wood accumulated on the stems should be largely irrelevant as a causal factor. Expressing the mortality rate relative to height increment implicitly links it to site quality.

Some of the plots contain a substantial amount of hardwoods (mean 3%, maximum 36%, by basal area). N corresponds to the pine component, but the mortality equation above might be expected to apply better to the total. If p_N is the proportion of pine in terms of number of trees, the total number N/p_N could be substituted for N in the equation. It is preferable, however, to use instead the proportion of pine by basal area, p, which is less erratic and more commonly available. We found from the data that $p_N \approx p^2$, so we substituted N/p^2 for N. We ignore changes in p over time, no consistent trends are evident in the data (see also Glover and Zutter, 1993). Including species composition produced only a marginal improvement in the fit, but it seems worthwhile for reasons of consistency.

The differential equation is separable,

$$(N/p^2)^{-a_3} \, \mathrm{d}(N/p^2) = -a_1 H^{a_2} \, \mathrm{d}H \ ,$$

and integrating both sides gives an invariant

$$(N/p^2)^{1-a_3} - a_1 \frac{a_3 - 1}{a_2 + 1} H^{a_2+1} = \text{constant} \ . \qquad (4)$$

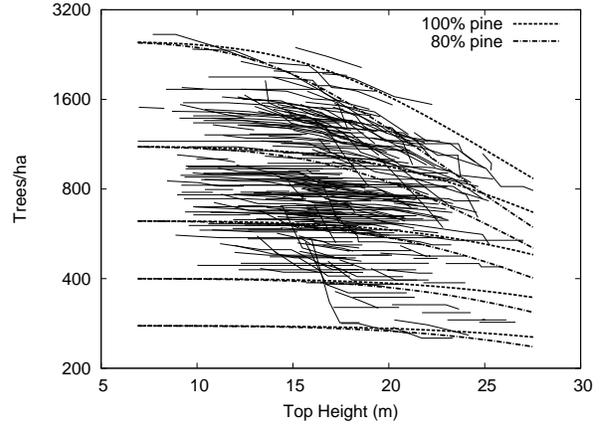Equating the invariant for times 1 and 2 gives the projec-

tion or transition function

$$N_2 = p^2 [(N_1/p^2)^{1-a_3} + a_1 \frac{a_3 - 1}{a_2 + 1}(H_2^{a_2+1} - H_1^{a_2+1})]^{1/(1-a_3)} \ . \qquad (5)$$

It predicts the change in N for time intervals in which no thinning occurred. Thinning causes an instantaneous decrease in N, with H left unchanged.

The parameters a_1, a_2 and a_3 were estimated by nonlinear least-squares on the logarithm of N projected by (5) over all the consecutive pairs of measurements (García, 2009)[1]. Both the observed H_2 and the value projected by the height growth model (2) resulted in similar parameter values. The estimates from the second option were chosen, being less affected by top height measurement and sampling noise, and being closer to how the model is used in practice: $a_1 = 1.754 \times 10^{-11}$, $a_2 = 3.642$, $a_3 = 2.518$.

The data and some model predictions are shown in Figure 3. From the data variability, it seems unlikely that substantially better results could be achieved with more complex models.

3.3. Basal area

Instead of predicting basal area (B) directly, we choose to model growth of the product $W \equiv BH$. Both volume and biomass per hectare are approximately linearly related to W, and compared to B its behavior is simpler and more easily interpreted. For convenience, we express increments

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[1] A reviewer noted that the logarithmic transformation causes the estimates of N to be biased, a common concern in the forestry literature. It is often suggested that a bias correction is needed, or better, that nonlinear least-squares should be used. However, there is no apparent reason why an unbiased estimate of N should be preferable to an unbiased estimate of its logarithm, stressing minimization of relative errors. More importantly, the distributional assumptions underlying estimator efficiency are more closely approximated on the logarithmic than on the original scale, where they would imply accepting that N can be negative.

relative to the top height increment, which, following Eichhorn (1904), are assumed to be independent of site quality. Graphing the residuals from the final model over site index confirmed that this assumption was satisfactory.

Below, we present and motivate a general form for the model equations, together with simpler more restricted versions that were tested. Components were thoroughly examined individually through graphical and regression methods to evaluate their performance and to obtain initial parameter estimates, but that detail is omitted here. Only the final parameter estimation with the whole model and the evaluation of simpler versions are shown. Full details are available in supplementary materials at http://forestgrowth.unbc.ca/lobdyn.

3.3.1. Growth and mortality

The increment can be partitioned into two components:

$$\frac{dW}{dH} = \text{gross increment} - \text{mortality} .$$

In pure closed-canopy stands, a fairly general model for the gross W-increment is

$$\text{gross increment} = b_1 H^{b_2} N^{b_3} ,$$

where the b_i are parameters to be estimated. As before, we prefer to exclude as drivers the accumulated stem-wood measures B or W.

In young or recently thinned stands that do not yet fully occupy the site, this increment is reduced by an "occupancy" factor Ω, an unobserved variable representing the effect of resource capture relative to that in a fully closed stand (e.g., light, nutrients, moisture). $\Omega = 1$ if the stand is fully closed. In addition, in stands with a hardwood component the increment is reduced by the factor p, the proportion of pine by basal area (or by W).

Occupancy is analogous to the proportionality between growth or photosynthesis and intercepted solar radiation first observed by Monteith (1972), and Monteith and Moss (1977). Many process-based models assume a strongly nonlinear relationship based of physiological measurements, although numerous studies have confirmed a linearization when integrating over time (Ruimy et al., 1995; Medlyn, 1998; Rosati and Dejong, 2003). In loblolly pine, linear trends are reported by Dalla-Tea and Jokela (1991), and Allen et al. (2004). It may be easier to think of Ω as (above- and below-ground) interception, but it can be seen more generally as an abstract representation of the relative effect of resource capture on growth, and precise knowledge of relationship forms or underlying mechanisms is not required.

The mortality rate, in units of W, can be written as

$$\text{mortality} = -k\frac{W}{N}\frac{dN}{dH} = -kW\frac{d\ln N}{dH} .$$

The quantity k is the mean size of dying trees relative to the mean size W/N of live trees. It might be taken as

constant or, more generally, as proportional to powers of H and/or N.

The most general basal area increment model considered here is therefore of the form

$$\frac{dW}{dH} = b_1 p\Omega H^{b_2} N^{b_3} + b_4 H^{b_5} N^{b_6} W \frac{d\ln N}{dH} . \quad (6)$$

In general, the differential equation (6) has to be integrated numerically. A simple closed-form solution exists in the special case where k is constant and $b_3 = k$, that is,

$$\frac{dW}{dH} = b_1 p\Omega H^{b_2} N^{b_3} + b_3 W \frac{d\ln N}{dH} \quad (7)$$

(García, 2011b, see below). We fitted and compared both model forms, as well as some more restrictive options.

3.3.2. Occupancy and closure

Occupancy is low in young stands, and gradually increases approaching 1 when canopy closes. Similarly, a thinning reduces site occupancy depending on thinning intensity, until the canopy recovers and closes again. We assume that the rate of closure initially depends on H in the same way as the gross increment, and decreases to zero as full closure is approached:

$$\frac{d\Omega}{dH} = c_1 p H^{b_2}(1 - \Omega) .$$

More complex models are possible, but this simple one has given good results (García, 2011b).

Integration gives the invariant

$$(1 - \Omega)\exp(\frac{c_1}{b_2 + 1}pH^{b_2+1}) = \text{constant} , \quad (8)$$

and transition function

$$\Omega_2 = 1 - \exp[-\frac{c_1}{b_2 + 1}p(H_2^{b_2+1} - H_1^{b_2+1})](1 - \Omega_1) . \quad (9)$$

With this occupancy model, it is shown that (7) gives an invariant

$$WN^{-b_3} - b_1(\frac{p}{b_2 + 1}H^{b_2+1} - \Omega/c_1) = \text{constant} \quad (10)$$

(as can be verified by differentiation), from where,

$$W_2 = \{W_1 N_1^{-b_3} + b_1[\frac{p}{b_2 + 1}(H_2^{b_2+1} - H_1^{b_2+1}) - $$
$$(\Omega_2 - \Omega_1)/c_1]\}N_2^{b_3} . \quad (11)$$

Thinning reduces the amount of foliage and roots approximately in proportion to the basal area or W removed, although occupancy does not decrease at the same rate (see below). Let the *relative closure* R represent the amount of foliage and fine roots present as a proportion of that in a fully closed stand. Most often $R \approx 1$ before thinning, and the R after the thinning then coincides with the proportion of basal area that is left. More generally,
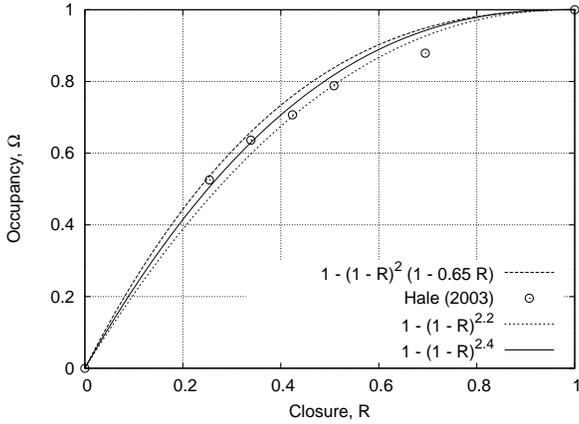
Figure 4: Relationships between occupancy and relative closure. The data points are measurements of relative light interception over thinning residual basal area fraction in Sitka spruce, from Hale (2003). The upper curve was indirectly inferred from growth in radiata pine, and the lower curve was assumed in the Scube spruce growth model of García (2011b). The intermediate curve is used here.

the R before thinning is multiplied by the basal area ratio, i.e.,

$$R_{\text{after}} = \frac{B_{\text{after}}}{B_{\text{before}}} R_{\text{before}} \ . \qquad (12)$$

This thinning basal area ratio usually differs from the thinning N-ratio, and if both are not known one can be estimated from the other for "typical" thinnings as indicated in Section 3.4.

To predict growth following the thinning it is necessary to know the occupancy Ω (the proportion of resources captured), that varies non-linearly with R. At low levels Ω is proportional to R, but a light thinning has little effect on resource capture. The relationship is shown in Figure 4. We shall use

$$\Omega = 1 - (1 - R)^{2.4} \ , \qquad (13)$$

intermediate between the curves for radiata pine and for the more tolerant spruces. Similar curves for light interception over leaf area index in loblolly pine are shown by Dalla-Tea and Jokela (1991), and Allen et al. (2004). Further direct experimentation would be interesting, but for our purposes an exact relationship is not critical.

For projecting growth from planting, R may be assumed to start as a small amount per tree. It is convenient to initialize the state variables at breast height, with $H = 1.3$, $N = N_b$ assumed known, $W = BH = 0$, and $R = \min\{N_b/c_2, 1\}$. The parameter c_2 represents a breast-height density at which the stand would be fully closed. The initial occupancy is

$$\Omega_b = 1 - (1 - \min\{N_b/c_2, 1\})^{2.4} \ . \qquad (14)$$

3.3.3. Parameter estimation and model selection

The model was fitted based on projections over pairs of consecutive measurements, what Gadow and Hui (1999) call *interval data*. Interval lengths were 3 years, except

in the instances where measurements had been removed in data screening. At breast height both $H = 1.3$ and $B = 0$ are known, and the generally small loss of trees up to the first measurement can be estimated with the mortality model (5). This point provided an additional interval for each plot, from breast height to the first measurement. These initial intervals, important for better modelling early growth, varied in length between 8 and 22 years, with an average of 15 years. The initial breast-height occupancy was calculated with (14).

Given the observed state at the start of an interval, W was predicted using either (11) for the integrable model (7), or numerical integration in the case of the fully parametrized version (6), together with (2), (5), and (9). Thinnings reduced R in proportion to the basal area removed (equation 12). Parameters were estimated by minimizing the root mean squared error (RMSE) of the differences between observed and predicted basal area.

All calculations were performed in the R statistical system (R Development Core Team, 2006; Venables and Ripley, 2002). The RMSE was minimized with the unconstrained optimization algorithm implemented by the BFGS option of the *optim* function. The R package *deSolve* (Soetaert et al., 2010) was used for numerical integration of the differential equation (6).

This is a relatively simple least-squares approach, where the non-overlapping intervals reduce the adverse effects of autocorrelation. More sophisticated methods could be used, e.g., simultaneous maximum likelihood or Bayesian estimates based on a system of stochastic differential equations, as in García (1984). Such methods can be shown to have desirable statistical properties if a certain model for the error structure is "true". However, if the stochastic assumptions are not strictly valid, as is always the case, there is no guarantee that such procedure will perform better. García (2011b) obtained essentially the same predictions with four different estimation methods, suggesting that an adequate representation of system dynamics might be insensitive to the details of stochastic modelling and statistical procedures.

Parameter estimates and fit statistics for increasingly restricted versions of the model are shown in Table 1. AIC (Akaike's information criterion) and BIC (Schwartz's Bayesian information criterion) adjust the negative log-likelihood penalizing for model complexity according to the number of parameters, and are commonly used in model selection (Venables and Ripley, 2002). In practice, computation was performed in the opposite order, starting with the simpler alternatives and using the parameter estimates as starting points for optimization in the next more general model.

Alternatives 1 and 2 correspond to models (6) and (7), respectively. The RMSE increases by less than 1% in going from the fully unconstrained model to the more convenient analytically integrable one, and the BIC improves.

In Alternative 3, $k = b_3$ was constrained to the range 0.4 to 0.5, more representative of the dead-tree relative

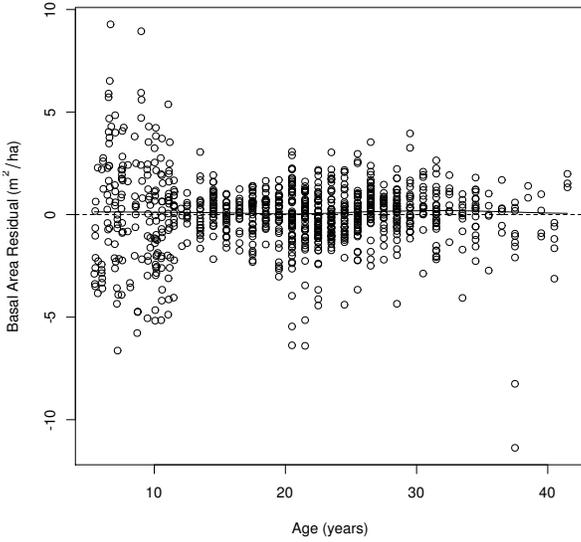| Param.	1	2	3	4
b_1	0.6092	0.8270	0.2798	0.2474
b_2	0.8233	0.8003	0.9542	*1*
b_3	0.3403	0.3057	*0.4*	*0.4*
b_4	1.925e-9	b_3	*0.4*	*0.4*
b_5	2.092	*0*	*0*	*0*
b_6	1.809	*0*	*0*	*0*
c_1	0.08056	0.08165	0.1155	0.1344
c_2	15582	14789	*40000*	*40000*
RMSE	1.703	1.718	1.730	1.731
Increase	—	0.88%	0.70%	0.06%
AIC	1049	1060	1069	1068
BIC	1088	1084	1084	1078

Figure 5: Basal area residuals for interval predictions. Continuous: nonparametric local regression curve. Dashed: zero line.

sizes observed in the preliminary analysis. This constraint caused the full-closure breast-height density c_2 to increase to unrealistically high values. Therefore, c_2 was also constrained to lie inside a more reasonable range of 4444 to 40000 trees/ha (average spacing of 0.5 to 1.5 m). The cost of using these better-supported values was small.

The estimated value for b_2, the exponent of H in the gross increment relationship, was close to 1. This value was found also in the Scube spruce model, and is implied by relationships observed in other species (García, 2011b). Reducing the number of free parameters by fixing $b_2 = 1$ (Alternative 4) had a negligible effect on the RMSE, and made this the best model according to the BIC.

Alternative 4 was chosen, considering accuracy, parsimony, robustness, and computational convenience. This is the same model form used by García (2011b).

Figure 5 shows the basal area residuals (observed minus

predicted), graphed over the age at the center of each interval. The curve ia a nonparametric local regression produced by the R *loess* procedure, with the default smoothing parameters in *scatter.smooth* (R Development Core Team, 2006; Venables and Ripley, 2002).

3.4. Model summary

The differential form of the model can be written as follows:

$$\frac{\mathrm{d}H}{\mathrm{d}t} = q(48.76/H^{0.07860} - 0.9271H) \tag{15a}$$

$$\frac{\mathrm{d}N}{\mathrm{d}H} = -1.754 \cdot 10^{-11} H^{3.642} N^{2.518}/p^{3.037} \tag{15b}$$

$$\frac{\mathrm{d}\Omega}{\mathrm{d}H} = 0.1344pH(1 - \Omega) \tag{15c}$$

$$\frac{\mathrm{d}W}{\mathrm{d}H} = 0.2474p\Omega HN^{0.4} + 0.4\frac{W}{N}\frac{\mathrm{d}N}{\mathrm{d}H} \tag{15d}$$

Recall that $W = BH$. A more conventional form in terms of the time derivatives could be obtained by substituting (15b) into (15d), and multiplying the last three equations through the first one.

This system of differential equations can be integrated analytically or numerically to project the state of the stand between any two points in time without thinnings inbetween. A thinning produces an instantaneous decrease in N and B, with H assumed unchanged, and the current R, related to Ω by $1 - \Omega = (1 - R)^{2.4}$, is reduced in proportion to B. Thinnings from above, in which H might be lowered, are not considered.

If either N or B after thinning are not known, relationships similar to those of García (1984, equations (10)–(12)) are used to estimate one from the other (see also Murray and von Gadow (1991)). Volumes and other quantities of interest can be estimated from regressions on the state variables.

When projecting from bare-land it is convenient to start from breast height, with $H = 1.3$, N assumed known or projected with (5), $B = 0$, and $R = N/40000$.

In this instance an analytical solution exists and numerical integration is not needed; the state can be projected over any time interval where disturbance does not occur with the transition functions (2), (5), (9), and (11). It is somewhat simpler and more efficient, however, to take advantage of the invariants. For an initial point at time t_1 these are

$$y_1 = [1 - (H_1/39.40)^{1.079}]\mathrm{e}^{qt_1}$$
$$y_2 = (p^2/N_1)^{1.518} - 5.737 \cdot 10^{-12} H_1^{4.642}$$
$$y_3 = (1 - \Omega_1)\exp(0.06721pH_1^2)$$
$$y_4 = W_1/N_1^{0.4} - 0.1237pH_1^2 + 1.840\Omega_1$$

Without thinnings between t_1 and t_2, the y_i do not change (in the model), so that the equations are valid with t_2 and the state at time t_2 substituted on the right-hand sides.
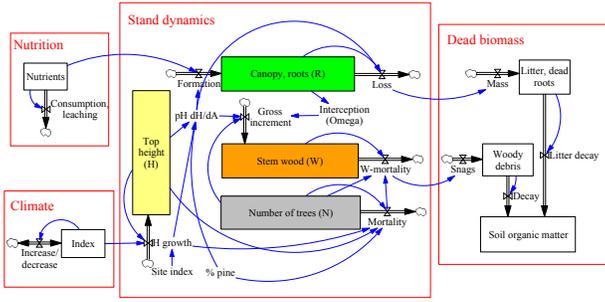
Figure 6: Implementation of the model differential equations in Vensim. The stand model is shown linked to blocks illustrating simplified nutrition, climate, and dead biomass components. Additional feedback or feed-forward links, e.g., between soil organic matter and nutrition, are possible but not shown. [To be reproduced in black-and-white in print]

The new state is recovered by solving the y_i equations sequentially:

$$H_2 = 39.40[1 - y_1 e^{-qt_2}]^{1/1.079}$$
$$N_2 = p^2/(y_2 + 5.737 \cdot 10^{-12} H_2^{4.642})^{1/1.518}$$
$$\Omega_2 = 1 - y_3 \exp(-0.06721 p H_2^2)$$
$$W_2 = N_2^{0.4}(y_4 + 0.1237 p H_2^2 - 1.840\Omega_2)$$

4. Implementation and extensions

Apart from the R functions used for parameter estimation and evaluation, the model has been implemented in two other forms: on System Dynamics visual simulation software, and on a spreadsheet. The programs and source code are freely available at `http://forestgrowth.unbc.ca/lobdyn`.

The central block of Figure 6 shows an implementation of the differential equations (15) in Vensim (`www.vensim.com/venple.html`). In the System Dynamics formalism the current level of a state variable is indicated by a box, and its rate of change given by the differential equation is represented as pipes with control valves. Arrows show influences, i.e., functional dependencies among variables. Other elements are auxiliary variables, parameters, or static relationships. Once the equations and initial values are specified, the system is simulated through numerical integration. Inputs and parameters can be altered in real time, and outputs are displayed in graphical or tabular form. This approach is useful for experimentation, and for communicating the structure and behavior of the system in a less technical way.

The spreadsheet simulator uses the invariants programmed as VBA macros, and is an adaptation of the one for the Scube model (García, 2011b). It is easy to use, and extensions or modifications are possible without advanced programming skills.

The system can be extended by interfacing to other environmental or management components through suitable input and output variables. E.g., the effects of genetic improvement can be approximated by altering the site index (Buford and Burkhart, 1987), or in this instance through scaling q by a certain factor. More generally, different factors ("multipliers") for growth in height and in diameter may be used (Carson et al., 1999; Adams et al., 2006).

The site productivity parameter q need not be constant, it can be made a function of time to reflect varying weather or climate (Fontes et al., 2010). More than one varying multiplier could be used if warranted. Similarly, Shula (1989) modelled forest fertilization through a multiplier dependent on levels of phosphorous. These levels could be altered by applying fertilizer, and did decay over time through leeching and consumption. Related methods were used for loblolly pine by Carlson et al. (2008).

Levels and rates from the various stand model components provide information useful for modelling biomass, carbon, and nutrient cycling.

Blocks depicting these processes and their links to the stand model are illustrated in Figure 6. Such a modular approach presents clear advantages, compared to a monolithic combination of detailed models of environmental processes and a simplistic growth model, or vice-versa.

5. Conclusions

A simple dynamical model for managed even-aged stands, originally developed with limited data for white spruce (García, 2011b), performed very well on a more extensive data set from loblolly pine plantations. Confidence in extrapolations outside the scope of the observations is improved by parsimony, and by following generally accepted biological principles. Application of similar models to other species and localities seems promising, in particular for data-poor situations where a small number of free parameters is desirable (Murray and von Gadow, 1993; Vanclay, 2010).

Having found parameter b_2 again not significantly different from 1 is intriguing. This is implied by the behavior observed by several authors on various species (see discussion and references in García, 2011b), but we know of no theoretical reason for it.

The model seems useful as a robust base-line building-block, for coordinating a modular development of additional environmental components.

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