A parsimonious dynamic stand model for interior spruce in British Columbia

Oscar García

University of Northern British Columbia
3333 University Way, Prince George, BC, Canada V2N 4Z9

Abstract

A whole-stand growth model, Scube, was developed for spruce-dominated, even-aged, natural and planted stands, using permanent sample plot data from the Sub-Boreal Spruce (SBS) biogeoclimatic zone of British Columbia, Canada. Available data were limited, with no information on mature planted stands or thinning treatments. A parsimonious model design, incorporating knowledge of stand dynamics and experience from other forests, made possible a logical reproduction of observed behavior and plausible extrapolations to other conditions. Scube consists of a system of four differential equations, describing the evolution of four state variables: top height, trees per hectare, basal area, and a stand closure indicator. Concepts of closure and site occupancy drive the behavior of young stands and the response to thinning. Parameters were estimated through numerical optimization of several residual functions, reflecting different projection interval types and weighting strategies. Differences in estimates among the various criteria were small. Calculations are facilitated through expressions that remain invariant in the absence of disturbances. The methods generalize the algebraic difference approach (ADA) and related forest modelling techniques, linking them to standard dynamical systems theory.

Keywords: Growth and yield, Canada, state-space, system dynamics, algebraic difference equations

1. Introduction

Together with lodgepole pine (*Pinus contorta* Douglas ex Louden), interior spruce is one of the main commercial trees in British Columbia, with both species accounting for most of the planting and wood production in the Province. Interior spruce refers to the predominant complex of white spruce (*Picea glauca* [Moench] Voss), Engelmann spruce (*Picea engelmannii* Parry), and their hybrids, where the individual species cannot be easily distinguished (Coates et al., 1994; Xie et al., 1998). It is prevalent in the Central Interior, where interest in it might increase after a mountain pine beetle epidemic that has killed much of the mature pine over the last decade (Walton, 2009). We focus on the economically important Sub-Boreal Spruce Zone (SBS), which occupies the northern half of the Interior Plateau (Meidinger and Pojar, 1991).

Reliable growth models are essential for effective long-term planning, sustainability assessments, and the evaluation of silvicultural alternatives such as planting density, thinning, and rotation length. We are particularly interested in forecasting the development of the extensive second-growth planted stands coming on stream, as they are the main target of management planning decisions. Two models have been available for spruce in the SBS: TASS and VDYP 7. TASS is based on assumptions about the crown and stem development of individual trees, with parameters adjusted by comparison of aggregated predictions with field data at a regional or national level (Mitchell, 1975; Di Lucca, 1998; Goudie, 1998). VDYP 7 is only applicable to natural stands (Ministry of Forests and Range, 2009c). This article describes Scube (named after *Stand, Spruce, SBS*), a whole-stand growth model for spruce-dominated even-aged interior spruce stands, developed using permanent sample plots from the SBS.

The model uses a state-space approach, now standard in many disciplines dealing with processes evolving in time (García, 1994, 2011; von Gadow and Hui, 1999, p. 47–49). Instead of trying to represent functions of time directly, one models rates of change for a number of state variables chosen to describe adequately the dynamics of the system. Integration produces global transition functions that predict the state at any time given the state at some other time. In forestry, univariate transition functions are often called "algebraic difference equations" (e.g., Tomé et al., 2006), although mathematically they are neither difference equations nor algebraic. The objectives were to faithfully reproduce the observed growth trends and to produce reasonable extrapolations for conditions not present in the data. To this effect, stands were modelled as a continuous-time dynamical system with four state variables, top height, trees per hectare, basal area, and a measure of stand closure, making sure that the equations for their rates of change were logically consistent, biologically sound, and parsimonious.

A high-level overview of Scube follows. Stand top height growth and its relationship to site quality are given by a site-index sub-model. For a given site, the rate of mortality or survival in trees per hectare is a function of number of trees and top height. The growth rate of stem volume or biomass per hectare equals gross increment minus mortality. This mortality

---

Email address: `garcia@unbc.ca` (Oscar García)

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. In this model occupancy and closure are unobserved variables, initialized at appropriate values and altered by thinning, although in the future similar variables could be quantified through remote sensing or other means. The rate equations just described, for height and volume or basal area growth, mortality, and rate of closure, are formulated as differential equations. In addition to the rate equations, several static relationships are used for site index calculations, to estimate changes from thinning, and to estimate volumes or other quantities of interest.

At each step, components were as far as possible tested against observations, experience with other forests, and/or generally accepted theory. Graphical analysis and regression with finite difference approximations were used to assess equation forms and to obtain initial parameter estimates. The estimates were refined through numerical optimization, using four alternative formulations of least-squares residuals for the complete model.

Scube's differential equations can be integrated analytically or numerically to project the state of a stand over time intervals of any length. A simpler and more efficient calculation procedure makes use of a set of four invariants, quantities that remain unchanged in the absence of stand disturbances. This can be seen as a multivariate generalization of principles implicit in forest modelling methods known as the algebraic difference approach (ADA).

The next section describes the data, followed by the development of the model components that specify the rate of change of each of the four state variables. The article continues with parameter estimation procedures and results, implementation, and some examples, including a comparison with existing spruce growth models. The final section discusses methodological and practical implications and relationships to other work. An extended report with full details and computer code is available from `http://forestgrowth.unbc.ca/scube`.

2. Data

Permanent sample plot (PSP) data from natural stands were provided by the Forest Analysis and Inventory Branch and from plantation experiments by the Research Branch of the British Columbia Ministry of Forests and Range. The Research Branch also provided stem-analysis data that were used in the site index / height growth sub-model, not discussed here (Hu and García, 2010). Zhengjun Hu carried out the extensive work of compilation, re-formatting, data screening, and calculation of plot-level variables, as part of his MSc thesis work at UNBC. Screening selected plot measurements with at least 70% spruce by basal area, single-layered, with a tree age range not larger than 20 years, unfertilized, and containing suitable site trees. The plots had to be at least 0.03 ha in size and have no evidence of severe wind or pest damage.

Naturally regenerated interior spruce stands are often highly irregular in their composition and in their age and spatial structure. For these reasons, the screening rejected a large proportion of the data initially available. Although the data may not be fully representative of a large part of the existing old-growth, our main interest lies in the development of the stands that have been planted over the last several decades, constituting the bulk of the future wood supply and the potential target of silvicultural interventions. Relatively regular natural stands are expected to provide useful information for ages not available in the young plantations.

The selected plots fall into two distinct groups: young stands, less than 25 years-old (breast-height age), all planted except for one plot of natural origin; and older stands, older than 25 years, all of natural origin. Statistics for the measurements in both groups and for the total are given in Table 1. *Initial N* is the estimated number of trees per hectare at breast height, and *Spruce %* is the percentage of interior spruce in a plot. In the natural plots, the most frequent secondary species was lodgepole pine, in 52% of the measurements, followed by trembling aspen in 22%.

The data are also shown in various ways in Figures 1, 2, 3, 8. All the planted data come from one large designed experiment, with replications at four sites. The experiment, established in 1967, compared interior spruce, lodgepole pine, and Douglas fir, planted at several spacings; details are available in Coopersmith et al. (1997). No data from thinned stands were available.

3. The Model

Clearly, the data coverage is far from ideal. In particular, predictions for mature planted stands and thinning simulations will necessarily be speculative. It is therefore important for the model to have a sound biological basis to borrow strength from the information on natural stands for plantation predictions and vice-versa. In addition, the number of parameters to be estimated should be kept low.

In the model, the condition (*state*) of a stand at any time is described by four state variables: top height (H, meters), trees per hectare (N), basal area (B, m^2/ha), and relative closure (R). Relative closure is not directly observed and represents the extent of the "resource capture apparatus", i.e., foliage and fine roots, relative to that in a fully closed stand (see below). The dynamical system model consists of one differential equation (DE) for each of the four state variables.

The height and mortality sub-models for $\mathrm{d}H/\mathrm{d}t$ and $\mathrm{d}N/\mathrm{d}t$, respectively, are described in detail elsewhere, and only a brief summary is given below (t is time, in years). This article focuses on the development of the B and R components.

The DEs are integrated to predict the state at any time, given the state at some other time, provided that there are no disturbances (e.g., thinning) in between. The initial R is estimated indirectly from the initial stand density, or from the observed degree of site occupancy in older stands. Calculations are sim-

Table 1: Measurement statistics.

	Mean	St.dev.	Min.	Quart. 1	Median	Quart. 3	Max.
Young stands (breast-height age < 25, $n = 57$), all but one planted							
Site index (base age 50)	19.7	1.0	18.4	18.7	19.6	20.5	21.6
B.H. age (years)	11.9	6.5	1.6	6.8	12.3	17.4	23.4
Top height (m)	5.4	2.4	1.7	3.6	5.4	7.2	10.3
Trees/ha	831	439	446	586	754	1026	3600
Basal area (m^2/ha)	3.68	3.83	0.02	0.47	2.18	6.42	13.68
Initial N	863	443	472	612	766	1088	3604
Spruce %	99.5	3.4	74.5	100	100	100	100
Meas. interval (yr)	4.96	0.86	4	5	5	5	10
Measurements / plot	4.39	0.87	2	4	5	5	5
Older stands (breast-height age > 25, $n = 85$), all of natural origin							
Site index (base age 50)	20.4	1.8	16.2	19.0	20.9	21.7	23.0
B.H. age (years)	51.9	12.1	27.5	44.5	52.0	59.5	76.5
Top height (m)	20.6	4.1	10.8	18.2	20.8	23.1	29.8
Trees/ha	1716	838	272	1111	1600	2133	5284
Basal area (m^2/ha)	35.7	8.3	13.1	29.5	36.9	41.2	52.1
Initial N	2709	2178	2869	1328	2364	3193	11616
Spruce %	81.2	6.5	71.7	76.2	78.4	86.3	95.3
Meas. interval (yr)	10.0	1.3	8	10	10	10	12
Measurements / plot	3.40	0.58	2	3	3	4	4
All stands ($n = 142$)							
Site index (base age 50)	20.1	1.6	16.2	18.9	20.3	21.5	23.0
B.H. age (years)	36.1	22.1	1.6	14.7	39.0	54.5	76.5
Top height (m)	14.6	8.3	1.7	6.4	16.9	21.2	29.8
Trees/ha	1367	829	272	882	1087	1832	5284
Basal area (m^2/ha)	23.0	17.1	0.0	4.1	27.7	38.3	52.1
Initial N	1981	1938	286	907	1145	2580	11616
Spruce %	88.4	10.5	71.7	78.2	88.0	100	100
Meas. interval (yr)	7.86	2.75	4	5	8	10	12
Measurements / plot	3.74	0.83	2	3	4	4	5

plified by making use of "invariants" (or first integrals), quantities that remain unchanged in the absence of disturbances.

For projections from bare land the model is started at breast height, with $H = 1.3$, $B = 0$, and $R = \rho N$, where ρ is a parameter.

3.1. Height Growth and Site Index

The growth rate equation is

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

or, in the more usual form of the Bertalanffy-Richards differential equation,

$$\frac{\mathrm{d}H}{\mathrm{d}t} = \frac{b}{c} H \left[\left(\frac{a}{H}\right)^c - 1 \right] .$$

The parameter c is 0.5829, $b \equiv q$ is a parameter that varies among plots according to site quality, and $a = 283.87 q^{0.5137}$ (Hu and García, 2010).

Integration of (1) gives the invariant

$$[1 - (H/a)^c] \mathrm{e}^{bt} = \text{constant} , \tag{2}$$

that can be used to predict H_2 at time t_2, given a height H_1 at time t_1, by equating the corresponding invariants and solving for H_2:

$$H_2 = a\{1 - [1 - (H_1/a)^c] \mathrm{e}^{-b(t_2 - t_1)}\}^{1/c} \tag{3}$$

(a global *transition function*).

The site quality parameter q can be related to the traditional site index, defined as the predicted height at 50 years breast-height age, by substituting the breast-height and age-50 values into (3):

$$\text{Site Index} = a\{1 - [1 - (1.3/a)^c] \mathrm{e}^{-49.5b}\}^{1/c} \tag{4}$$

(defining breast-height age as number of rings at breast height, breast height is reached at age 0.5, on average (Nigh, 1995)). This equation needs to be solved numerically for calculating a value of q given a site index estimate.

3.2. Number of Trees

The mortality (or survival) model is fully explained in García (2009). It uses a site-independent relationship for the mortality relative to height growth:

$$\frac{\mathrm{d}N}{\mathrm{d}H} = -4.5759 \cdot 10^{-15}\, H^{5.009} N^{2.9895} \; .$$

An equation for $\mathrm{d}N/\mathrm{d}t$ can be obtained dividing by the equation for $\mathrm{d}H/\mathrm{d}t$ above.

The invariant, written in terms of the average spacing $S \equiv 100/\sqrt{N}$, is

$$S^{3.979} - (0.07213H)^{6.009} = \text{constant} \; . \qquad (5)$$

Species composition was tried as an additional predictor, but there was no improvement.

3.3. Basal Area

3.3.1. Gross Increment

It is simpler to model growth for the product of basal area and height, BH. This is approximately linearly related to total volume or biomass per hectare, and for closed-canopy stands in a given site its increment varies less over time than the basal area increment (compare Figures 1 and 2).

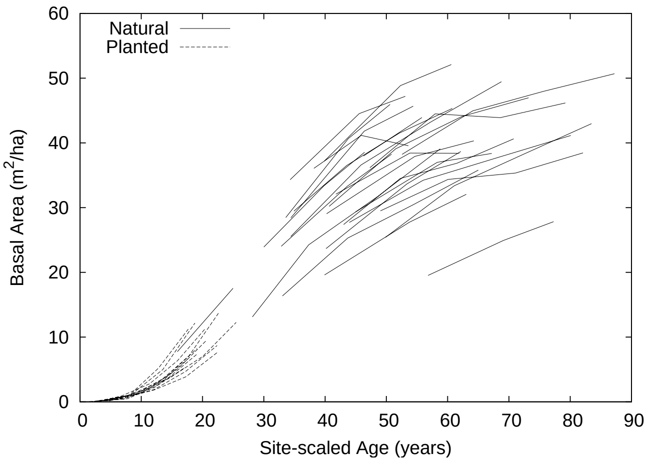

Figure 1: Sample-plot basal area over age. Consecutive measurements on a same plot are joined by lines. Ages scaled to a site index 20 equivalent.

One can write

$$\frac{\mathrm{d}BH}{\mathrm{d}t} = \text{gross increment} - \text{mortality} \; . \qquad (6)$$

Here *gross increment* and *mortality* are in units of BH per year. This mortality can be expressed as the product of the mortality in number of trees, the mean tree size, and a factor k representing the average relative size of dead trees:

$$\text{mortality} = -k \frac{BH}{N} \frac{\mathrm{d}N}{\mathrm{d}t} \; .$$

Values of k estimated for each measurement interval were found to be highly variable, ranging from 0.11 to 0.92, but not clearly related to any stand variables. The average weighted by number of dead trees per hectare was 0.299, and the model will use $k = 0.3$. Attempts at finding a better estimate in the final model showed that the sensitivity of predictions to a precise value of k was very low. The $k = 0.75$ assumed by García and Ruiz (2003) seems high, with informal tests on data from radiata pine, aspen and loblolly pine suggesting values in the 0.4–0.5 range. The lower value for spruce may reflect its higher shade tolerance.

Taking the mortality term to the left-hand side of (6),

$$\frac{\mathrm{d}BH}{\mathrm{d}t} - k \frac{BH}{N} \frac{\mathrm{d}N}{\mathrm{d}t} = \text{gross increment} \; ,$$

which can be written as

$$\frac{\mathrm{d}BHN^{-k}}{\mathrm{d}t} = N^{-k} \times \text{ gross increment} \; . \qquad (7)$$

This can be verified by expanding the derivative of the product $(BH) \times N^{-k}$. The combination BHN^{-k} is related to the accumulated gross increment in a way that avoids dealing directly with the mortality term.

3.3.2. Closed Stands

In a closed-canopy stand that fully utilizes the site potential, the gross BH-increment on the right-hand side of (7) can be modelled as some function of N and/or H. We prefer not to include B as a driving variable, because it seems doubtful that by some physiological mechanism the accumulation of (mostly dead) xylem on the stems should directly and significantly affect growth (García, 2009).

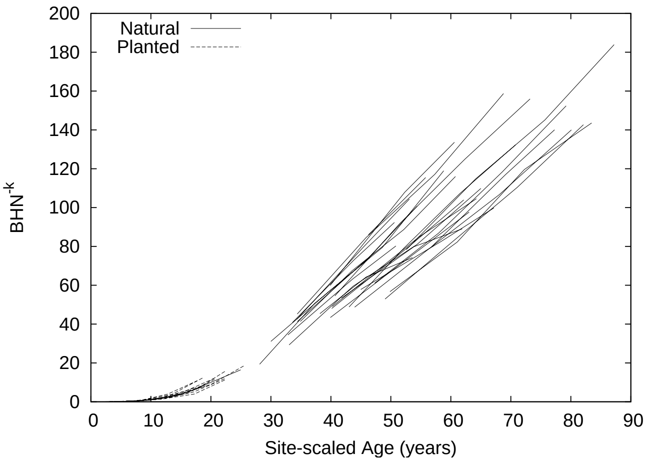

Figure 2: Observed trajectories from equation (7). Ages scaled to site-index 20 equivalent.

Figure 2 shows the changes in BHN^{-k} over time. Age has been scaled by a site-dependent factor to reduce the effects of site quality, as in García and Ruiz (2003). Once canopy closes, there are no indications of important changes in the slope given by equation (7). To analyze this further, the derivative in (7) was approximated by divided differences for each pair of consecutive measurements, and regressed over the mid-point values of N and/or H. Only measurements with $BH > 200$ were used to exclude young stands not yet fully occupying the site. No significant regressions were found, with the best estimate being $\mathrm{d}BHN^{-k}/\mathrm{d}t = 2.75$.

That would imply a BH gross increment proportional to $N^{0.3}$. García (1990) and García and Ruiz (2003) also found N to be the best predictor, with increments increasing with N. Such a model gave good results over the range of our data. However, extrapolation beyond about 100 years of (scaled) age often produced seemingly unnatural inflections in basal area trends. More plausible extrapolated behavior was obtained by modelling the gross increment relative to height increment,

$$\frac{\mathrm{d}BHN^{-k}}{\mathrm{d}H} = f(H) \, , \tag{8}$$

so that B does not keep increasing as H approaches its asymptote. This also eliminated the need for age site-scaling, assuming that Eichhorn's hypothesis about relationships between stand state variables being approximately independent of site quality is acceptable. Eichhorn's assumption has generated considerable controversy, a good review of which is contained in Holten-Andersen (1989, pages 107–114). It has been found that it can fail when applied over extensive areas, such as at the European level, but it can be a good approximation within smaller regions with less heterogeneous growing conditions. *Eichhorn's rule* has been used in the development of yield tables and growth models for Denmark (Holten-Andersen, 1989), New Zealand (Beekhuis, 1966), the UK (Hamilton and Christie, 1971), and British Columbia (Mitchell and Cameron, 1985; Mitchell et al., 2004). Graphing the residuals from our final model over site index indicated that any deviations from Eichhorn's assumption would be small relative to other sources of error.

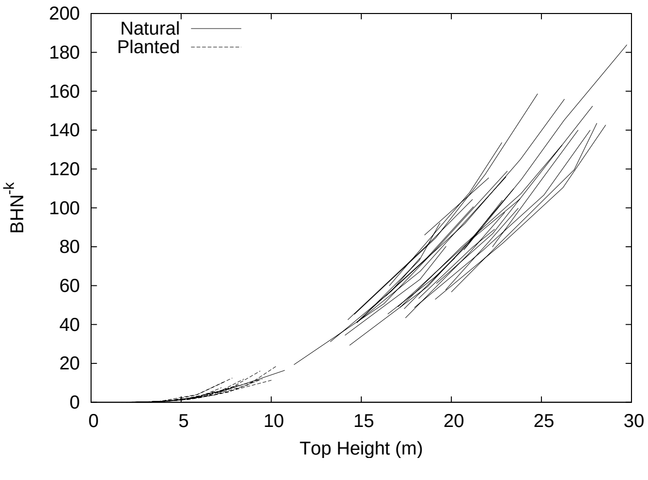

Figure 3: Observed trajectories from equation (8).

It is seen in Figure 3 that the slopes increase with H. Again using finite difference approximations and $BH > 200$, regressions for (8) confirmed no significant contribution from N. Closed-canopy data were available only from natural stands, which in the sample may contain as little as 72% spruce, averaging 81% (Table 1). Not surprisingly, the proportion of spruce was found to be a significant increment predictor, either using observed values for each measurement or plot averages. There were no consistent trends of species composition over time, so it was decided to use a plot average, calculated by dividing the sum of the spruce basal areas from all the plot measurements by the sum of the all-species basal area. The best predictor in (8) was $f(H) = 0.60pH$, where p is the proportion of spruce. For more flexibility, an exponent other than 1 was allowed in the model:

$$\frac{\mathrm{d}BHN^{-k}}{\mathrm{d}H} = \alpha p H^{1-\beta} \, , \tag{9}$$

with initial estimates $\alpha = 0.6, \beta = 0$.

3.3.3. Open Stands

Young stands, or stands that have been recently thinned do not yet have enough foliage and root extension to capture all the available site resources. Their growth rate will be a fraction Ω of that in a fully closed stand. That is, (9) changes to

$$\frac{\mathrm{d}BHN^{-k}}{\mathrm{d}H} = \alpha p \Omega H^{1-\beta} \, , \tag{10}$$

where the "relative occupancy" Ω is 1 for fully closed stands. Equation (9) becomes a special case of (10).

In open stands Ω increases as the amount of foliage and fine roots build up until reaching some dynamic equilibrium where $\Omega = 1$. Let R, called *relative closure*, represent the extent of this "assimilation apparatus" as a proportion of the maximum. It may be useful to think of R as amount of foliage (e.g., leaf area index), and of Ω as light interception, although these variables can also represent below-ground processes, and we do not need to be precise about the exact mechanisms. Formally, Ω is defined as the ratio of gross increment to the gross increment in a fully closed stand. R is a measure of foliage and fine roots relative to that in a closed stand, such that it is initially proportional to the number of trees in the absence of competition, and decreases in proportion to the basal area removed when thinning.

Ω and R are non-linearly related. At low levels, resource capture increases in proportion to the assimilating material, but near the maximum an increase in R has a negligible effect on Ω: leaves at the base of the canopy make a small or even negative contribution to net photosynthesis, and it is known that moderate thinning has a relatively minor effect on light interception and per hectare growth rates (e.g. Beekhuis, 1966; Hale, 2003). The only attempt at determining such a relationship directly at the stand level seems to be the work of Hale (2003), in which light interception was measured after removing successively increasing proportions from a Sitka spruce stand in Scotland. Figure 4 compares a curve inferred from modelling the development of intensively managed radiata pine plantations (García, 1989, 1990), the measurements from Hale (2003), and the curve

$$\Omega = 1 - (1 - R)^{2.2} \tag{11}$$

to be used here. It will be seen that the exact relationship is not critical.

Integration of (10) depends on the rate of closure and is discussed below.

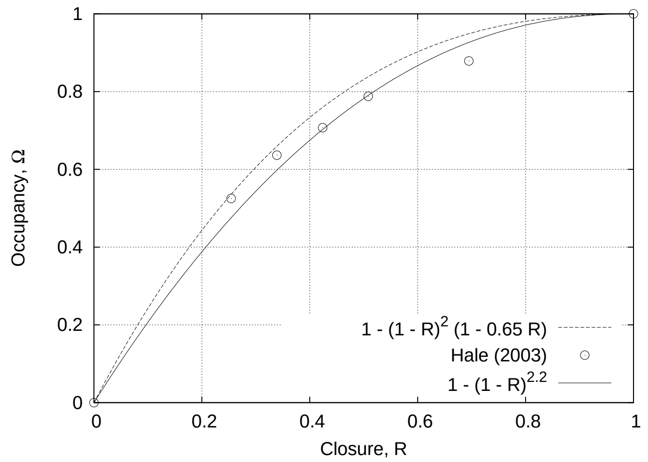

Figure 4: Relationships between relative occupancy and relative closure. Dashed curve inferred from radiata pine growth (García, 1989, 1990). Data points are measurements of relative light interception over thinning residual basal area fraction in Sitka spruce (Hale, 2003). The continuous curve is used here.

3.4. *Relative Closure*

It remains to model the increase of R (or of Ω) in less than fully-closed stands. It makes sense to assume that initially the increment of R is similar to the gross increment in (8)–(10), later declining to 0 as full closure $R = 1$ is approached and the canopy base starts to lift:

$$\frac{\mathrm{d}R}{\mathrm{d}H} = g_1(R)\Omega f(H) \,,$$

or, equivalently,

$$\frac{\mathrm{d}\Omega}{\mathrm{d}H} = g_2(\Omega)\Omega f(H) \,,$$

where g_1 and g_2 are decreasing functions such that $g_1(1) = g_2(1) = 0$. Writing $\Omega g_2(\Omega) \equiv g(\Omega)$,

$$\frac{\mathrm{d}\Omega}{\mathrm{d}H} = \alpha p g(\Omega) H^{1-\beta} \,. \tag{12}$$

In this model neither R nor Ω is observed; they are assumed to equal 1 in closed stands, or they are otherwise projected with the equations above, starting from suitable initial values. Before competition begins, R should be proportional to the number of trees. Therefore, we initialize R at breast height as

$$R_b = \min\{\rho N_b, 1\} \,, \tag{13}$$

where N_b is the number of trees per hectare at breast height and ρ is a parameter to be estimated. On thinning, the current R is reduced in proportion to the basal area removed. R is converted to Ω with (11), and then projected with (12).

Equation (12) is separable,

$$\frac{\mathrm{d}\Omega}{g(\Omega)} = \alpha p H^{1-\beta}\,\mathrm{d}H \,,$$

and given $g(\Omega)$, both sides can be integrated to obtain an invariant

$$\int \frac{\mathrm{d}\Omega}{g(\Omega)} - \frac{\alpha p}{2-\beta} H^{2-\beta} = \text{constant} \,. \tag{14}$$

Equation (10) can now be integrated in a number of ways, a convenient and numerically stable one being to write it as

$$\mathrm{d}BHN^{-k} = \alpha p H^{1-\beta}\,\mathrm{d}H - \alpha p(1-\Omega)H^{1-\beta}\,\mathrm{d}H \,,$$

and substituting $\mathrm{d}H$ from (12) into the second term on the right-hand side,

$$\mathrm{d}BHN^{-k} = \alpha p H^{1-\beta}\,\mathrm{d}H - \frac{1-\Omega}{g(\Omega)}\,\mathrm{d}\Omega \,.$$

Finally, integrating,

$$BHN^{-k} - \frac{\alpha p}{2-\beta} H^{2-\beta} + \int \frac{1-\Omega}{g(\Omega)}\,\mathrm{d}\Omega = \text{constant} \,. \tag{15}$$

Three functional forms for $g(\Omega)$ were tested:

Linear:

$$g(\Omega) = \gamma(1-\Omega) \,, \tag{16}$$

Quadratic:

$$g(\Omega) = \gamma\Omega(1-\Omega) \,, \tag{17}$$

Two-parameter:

$$g(\Omega) = \gamma(1+1/\delta)(1-\Omega)^{1+\delta/(\delta+1)}[1-(1-\Omega)^{1/(\delta+1)}]^{1-\delta} \,, \tag{18}$$

where γ and δ are parameters. The third form, with two free parameters, was chosen so as to be flexible, but at the same time give closed-form solutions for the integrals in (14) and (15); the derivation is available from `http://forestgrowth.unbc.ca/scube`.

Naturally regenerated stands have a more irregular spatial pattern of tree locations than planted ones and might be expected to take longer to occupy the site. To allow for this possibility, a model variation with different values of γ in (18) for natural and for planted stands was tried.

3.5. *Summary of Projection Equations*

For brevity, calculations are shown only for the *linear* closure rate sub-model (16), the one finally chosen.

To efficiently project the state of a stand between times t_1 and t_2, one can compute the invariants at t_1 and then invert them to recover the state at t_2. The invariants, from (2), (5), (14), and (15), are:

$$\begin{aligned}
y_1 &= [1-(H_1/a)^c]\exp(bt_1) \\
y_2 &= (100/\sqrt{N_1})^{3.979} - (0.07213H_1)^{6.009} \\
y_3 &= (1-R_1)^{2.2}\exp[\gamma\,\varphi(H_1)] \\
y_4 &= B_1H_1N_1^{-k} - \varphi(H_1) + [1-(1-R_1)^{2.2}]/\gamma
\end{aligned}$$

where $\varphi(H) = \frac{\alpha p}{2-\beta}H^{2-\beta}$. The exponential of (14) has been used to avoid difficulties when $\Omega \to 1$. Without thinnings or other disturbances between t_1 and t_2, the y_i do not change, so that the equations are valid with t_2 and the state at time t_2 substituted on the right-hand sides. The new state is obtained by solving the y_i equations sequentially:

$$\begin{aligned}
H_2 &= a[1 - y_1 \exp(-bt_2)]^{1/c} \\
N_2 &= 10000/[y_2 + (0.07213H_2)^{6.009}]^{2/3.979} \\
R_2 &= 1 - \{y_3/\exp[\gamma\,\varphi(H_2)]]\}^{1/2.2} \\
B_2 &= N_2^k\{y_4 + \varphi(H_2) - [1 - (1 - R_2)^{2.2}]/\gamma\}/H_2
\end{aligned}$$

Somewhat simpler equations can be obtained by using Ω as a state variable instead of R.

As already mentioned, for projections from bare land the state is initialized at breast-height age with $H_1 = 1.3$, N_1 assumed known, $B_1 = 0$, and R_1 from (13). In case of thinning, there is an instantaneous reduction in N and B, with the top height H assumed unchanged. R is reduced in proportion to the basal area removed. If either the residual B or residual N is not known, the relationships in García (2005) can be used to estimate one from the other for "typical" thinnings.

When projecting an existing stand, R_1 is not available. One can use $R_1 = 1$ for closed-canopy stands, e.g., if the base of the crowns is rising. Following a thinning, R_1 approximately equals the fraction of basal area remaining. For young open stands, R_1 may need to be estimated through a projection from breast-height.

Usually $t_2 > t_1$, but the procedure is also mathematically valid going back in time, which is sometimes useful. Some care is needed, however, because the back-projection of R can be numerically unstable if R_1 is close to 1.

3.6. Volumes

Volumes per hectare can be estimated given the state variables H, N, and B. Most stand volume tables use only H and B (see, for instance, Husch et al., 2003, Sec. 8–6.1, van Laar and Akça, 2007, Sec. 7.3). Beekhuis (1966) pointed out, however, that after thinning the volume per unit of basal area rises slightly because of the greater average height of the trees left; including also N in the volume function can account for this. Augmenting the data used here with single-measurement plots, Zhengjun Hu obtained the following regression for the volume to basal area ratio:

$$\frac{V}{B} = 0.2716 + 0.3370H + 6.5262\frac{H}{N} \tag{19}$$

($n = 252$, SE $= 0.3684$). This equation is of the same form as the one in García (2005), but the coefficients are considerably different. García (2005) used the TIPSY spruce data base, that was generated by simulation with the TASS growth model (Mitchell, 1975; Di Lucca, 1998; Mitchell et al., 2004). For similar values of the state variables and within the range of our data, volumes in the simulated plots are on average 6% to 12% lower than those observed in the SBS permanent sample plots. The reasons for the discrepancy are not clear; it may be due to different tree volume calculation procedures, or to differences between the simulated and observed tree size distributions. Equation (19) is used in the current model implementation, although further investigation might be warranted.

Merchantable volumes are being estimated with ratios of merchantable to total volume from García (2005).

4. Parameter Estimation and Results

Statistical parameter estimation optimizes some criterion of fit, given a certain stochastic model for the observations. In this instance, a reasonable model for the variability could be fairly complex, possibly involving environmental perturbation of growth rates, giving rise to stochastic differential equations, compounded with sampling and measurement errors in a hierarchical structure (e.g. Seber and Wild, 2003, Sec. 7.5). Any optimal properties and error estimates are conditional on the assumed model being "true", but little is known about the consequences of model misspecification. A more heuristic and direct approach was used here, trying to obtain a good over-all fit to the observations while avoiding biases for particular growing conditions.

Estimation in dynamical systems can be based on projections over a variety of time intervals (Ch.VIII in Bard, 1974; Borders et al., 1988; García, 1994; Seber and Wild, 2003, Sec. 7.5). The model parameters were estimated by minimizing a root mean square error (RMSE) calculated in four different ways:

1. *From breast height.* Many applications require predictions starting from bare land, and model evaluation typically looks at the quality of such predictions (Goulding, 1979; Vanclay and Skovsgaard, 1997). It seems natural, therefore, to minimize the deviations for each measurement occasion with respect to the predictions calculated starting from breast height.
2. *Shortest intervals.* Observed sizes on a same plot are highly correlated, because they arise from accumulated growth over overlapping time intervals. Deviations for projections starting from the first point in each pair of consecutive measurements are more nearly independent, leading to better statistical properties (Borders et al., 1988; Seber and Wild, 2003, Sec. 7.5.1). On the other hand, bias might accumulate over longer time spans if the model is poor. The RMSE included the intervals from breast height to the first measurement in each plot.
3. *Weighted shortest.* Although the deviations for non-overlapping intervals might be considered as statistically independent, their variances vary with the interval length. Under certain conditions, the variance increases roughly proportionally to time, and an RMSE with inverse weighting by interval length would be favored by statistical theory (Seber and Wild, 2003, Appendix C). In this instance, the effect is mainly a reduced contribution of the long intervals from breast height to first measurement in the natural-origin plots, which might not be desirable when the model is not "true".

4. *Weighted from breast height.* Finally, an RMSE was calculated with breast-height predictions as in criterion 1, but with the inverse time difference weighting of criterion 3. This might to some extent attenuate the redundancy from interval overlapping.

In the case of the older sample plot appearing below the others toward the bottom-right of Figure 1, projections were started from its first measurement, because it seemed likely that it may have suffered some disturbance earlier in life.

The RMSE calculations were programmed in R (R Development Core Team, 2009), and the values minimized using the BCFGS method of function `optim`.

Allowing different rate-of-closure parameters (γ), as discussed at the end of the section on Relative Closure, resulted in an earlier estimated closure in natural than in planted stands, contrary to expectations. The reduction in RMSE compared to a common γ was small. Gaps in the natural spruce regeneration can promote the emergence of other species, so that the inclusion of the species composition variable p in the model may already account sufficiently for any growth differences. Therefore, only model variants with a single γ parameter are considered in what follows.

When assessing degree of fit, the complexity of the models needs to be taken into account. Akaike's Information Criterion (AIC) and Schwartz's Bayesian Information Criterion (BIC), are commonly used for this purpose. The AIC and BIC are defined in terms of the likelihood, but assuming independent normal residuals they can be calculated from the RMSE, the number of parameters m, and the number of observations n, as

$$2n \ln \text{RMSE} + \lambda m \ ,$$

where the factor λ that penalizes the number of parameters is 2 for the AIC and $\ln n$ for the BIC (e.g., R Development Core Team, 2009; Venables and Ripley, 2002, p. 174). The values are defined only up to an arbitrary constant, so that only differences are meaningful. Although the distributional assumptions are never "true", these indices should still be useful for comparison, at least with criteria 2 and 3.

The calculated basal area RMSE, AIC and BIC are given in Table 2 for the four fitting criteria, and for the model variants in decreasing order of complexity: the *two-parameter* rate-of-closure model of equation (18), the *linear* (16), and the *linear* with the β parameter of (10) fixed at 0. The *quadratic* model (17) is omitted, because the RMSE was consistently higher than that of the *linear*, with the same number of parameters. Values are not comparable across fitting criteria, because they correspond to different kinds of residuals.

It is seen that the additional flexibility of the two-parameter closure rate model, compared to the linear one, made little or no difference to the fit as measured by the RMSE; both the AIC and the BIC favor the later. Graphs show that the predicted Ω *vs* H trajectories had similar shapes. Basal area or volume predictions depend on the integral of these, causing rather different rate equations to be indistinguishable in practice.

All the estimated β values were close to 0, and fixing $\beta = 0$ was largely inconsequential, agreeing with the earlier preliminary analysis. Overall, the fit statistics point to the simplest model as the most appropriate for these data. Extensive graphical analysis confirmed that residuals and predictions for all the model variants were very similar.

Parameter estimates for the *linear* $\beta = 0$ version obtained according to each of the four fitting criteria are given in Table 3. For comparison, the RMSE from each fit under the other criteria were also computed, and the relative differences with respect to the minimum are shown as percentages in the last 4 columns of the Table.

Graphical examination showed generally negligible differences in predictions among the 4 parameter sets, with only criterion 1 slightly different from the others in some instances. Worsening in degree of fit according to criteria different from the one used in estimation was slight (columns C1–C4 in Table 3), indicating predictions that are robust under the various estimation methods. The parameters from criterion 2 were chosen for the final model.

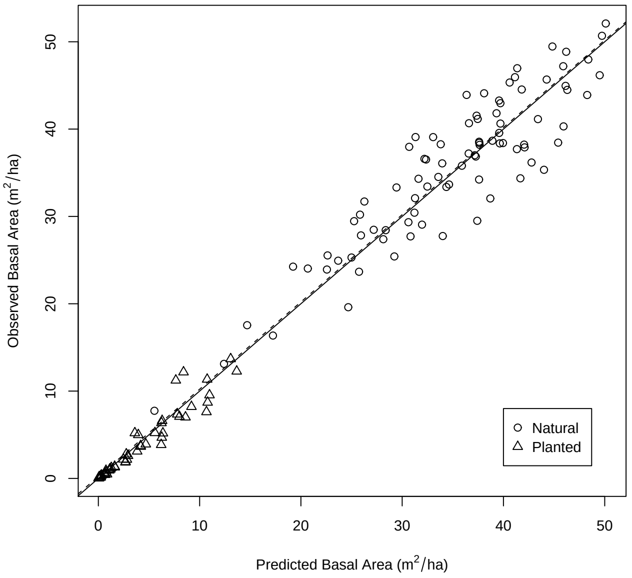

Figure 5: Observed and predicted basal areas. Predictions starting from breast height. Linear regression (dashed) not significantly different from the identity line (solid).

An extensive analysis of residuals was performed, both graphically and by fitting trend surfaces. Although variability was high, no systematic biases were detected. A commonly used display and measure of model performance, recommended by Vanclay and Skovsgaard (1997), tests a linear regression of observed *vs.* predicted data (Figure 5). A statistically equivalent but more visually stringent method is to graph the residuals on the y-axis; this is done for the relative residuals in Figure 6.

Table 4 gives an idea of the differences that can be expected in individual plot predictions. The statistics are for observed minus predicted from breast height, using all the available measurements, and are tabulated as percentages of the mean. V is total volume per hectare, estimated by (19).

Table 2: Root mean square eror, AIC, and BIC statistics for three model forms.

	Two-par., eq. (18)			Linear, eq. (16)			Linear, $\beta = 0$		
Criteria	RMSE	AIC	BIC	RMSE	AIC	BIC	RMSE	AIC	BIC
1 (from b.h.)	2.978	317.8	332.5	2.994	317.3	329.1	3.009	316.6	325.5
2 (shortest int.)	1.919	193.8	208.5	1.919	191.9	203.7	1.923	190.4	199.3
3 (weighted sh.)	1.213	64.6	79.3	1.216	63.2	75.0	1.217	61.3	70.1
4 (weighted b.h.)	1.631	147.9	162.7	1.642	147.8	159.6	1.643	146.0	154.9

Table 3: Parameter estimation results under 4 criteria. Columns C1–C4 show the % RMSE increase for the other criteria.

Crit.	α	γ	$\rho \times 10^6$	C1	C2	C3	C4
1 (from b.h.)	0.5270	0.11663	0.159	–	1.1	4.3	0.7
2 (shortest int.)	0.5345	0.09662	1.815	0.9	–	1.4	0.3
3 (weighted sh.)	0.5512	0.08569	1.621	2.7	1.1	–	1.6
4 (weighted b.h.)	0.5323	0.10098	5.026	0.5	0.2	1.9	–

Table 4: Residual statistics for plot predictions from breast height

	Age < 25				Age > 25			
Variable	Mean	Mean deviation %	Mean abs. deviation %	RMSE %	Mean	Mean deviation %	Mean abs. deviation %	RMSE %
H	5.37	0.81	4.26	5.16	20.6	-0.077	1.95	2.43
N	780.8	-4.11	4.11	6.14	1733	0.255	6.59	11.3
B	3.61	-6.45	18.7	30.7	35.8	1.296	8.56	10.6
V	10.8	-4.89	16.8	29.9	270	0.611	9.98	12.7

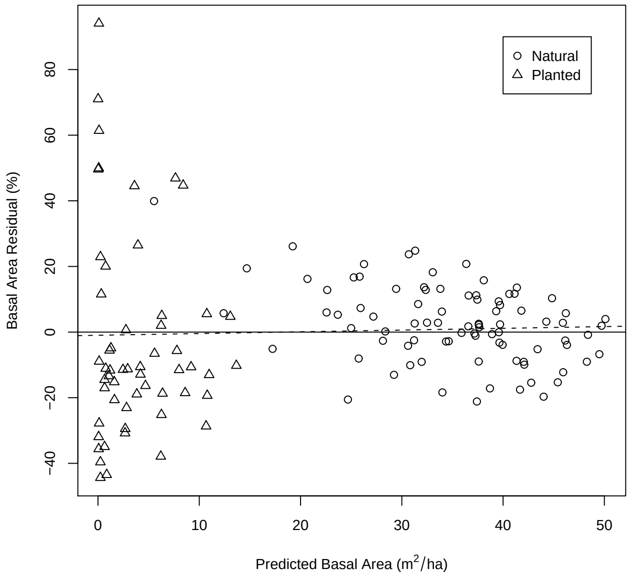

Figure 6: Relative basal area residuals, predictions from breast height (observed minus predicted, as percentage of the observed value). Linear regression (dashed) not significantly different from 0.

5. Implementation and Examples

Various computer implementations of the model are possible. An interactive simulator implemented in Microsoft Excel with VBA macros is available from `http://forestgrowth.unbc.ca/scube`. Code based on the macros or on the R functions used in parameter estimation can be easily embedded into decision support systems or other applications.

The invariants approach provides explicit and computationally efficient solutions. It can be useful, however, to write down the model differential equations in the more traditional form used in dynamical systems theory. There are 4 differential equations, for the 4 state variables H, N. R, and B:

$$\frac{\mathrm{d}H}{\mathrm{d}t} = 46.167 q^{1.2994} H^{0.4171} - 1.7156 qH \tag{20a}$$

$$\frac{\mathrm{d}N}{\mathrm{d}H} = -4.5759 \cdot 10^{-15} H^{5.009} N^{2.9895} \tag{20b}$$

$$\frac{\mathrm{d}R}{\mathrm{d}H} = 0.023474 pH(1 - R) \tag{20c}$$

$$\begin{aligned}\frac{\mathrm{d}B}{\mathrm{d}H} &= 0.53449 pN^{0.3}[1 - (1 - R)^{2.2}] - B/H \\ &\quad - 1.3728 \cdot 10^{-15} H^{5.009} N^{1.9895} B\end{aligned} \tag{20d}$$

The last three equations can be expressed as the usual derivatives with respect to t through multiplying by (20a). Initial conditions at breast height are $H = 1.3$, $N = N_{\mathrm{bh}}$, $R = 1.815 \cdot 10^{-6} N_{\mathrm{bh}}$, and $B = 0$. The parameter p is the proportion of spruce, assumed constant, and q represents site quality, with $q = 0.02028$ for site index 20.

The DE system (20) can be numerically integrated in visual simulators like Vensim, Stella, or Simulink, that follow System Dynamics principles (e.g., Ford, 1999, Ch. 2). This can be useful for experimentation and can help to better understand the structure of the system. Figure 7 is a System Dynamics diagram using the free version of Vensim (`www.vensim.com/venple.html`). The boxes represent the state variables (*stocks*, *levels*), and the double-arrow "pipes" with control "taps" represent their rates of change over time (*flows*, *rates*). Arrows indicate influences, i.e., variable dependencies. Symbols not enclosed in boxes are parameters, or input, output, or intermediate variables. The software can display graphs or tables for any of the variables, with inputs and parameters changeable through keyboard entry or graphical sliders in real-time.

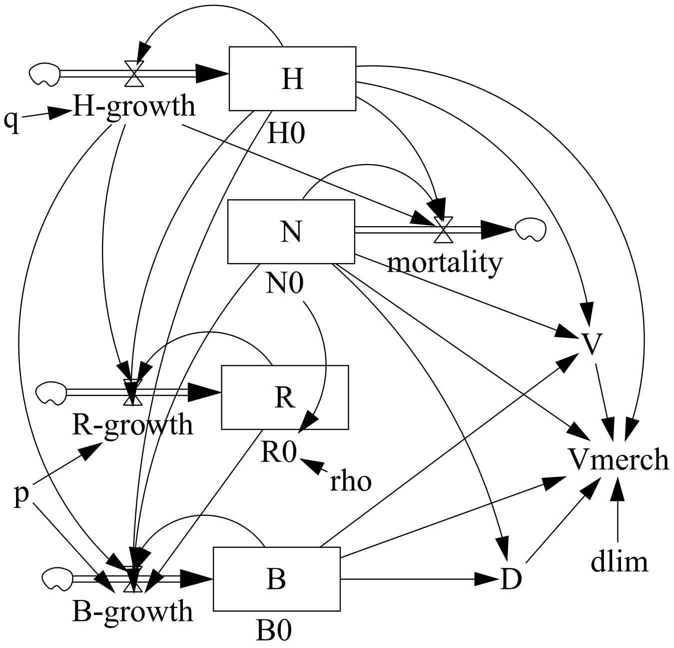

Figure 7: System Dynamics diagram of the model in Vensim (see text).

Verification that the R, Excel, and Vensim implementations all produced the same results gives ample confidence in the correctness of the equations, and in that the programs perform as intended.

Two other models are available for predicting spruce growth in the SBS Zone. VDYP 7 is a whole-stand growth model for natural stands of various species in BC (Ministry of Forests and Range, 2009c). Predictions starting from bare land produced very low basal areas and volumes, compared to our PSP data. TASS (Mitchell, 1975; Di Lucca, 1998) is a distance-dependent individual-tree growth model for even-aged stands, with versions for natural and for planted white spruce in the BC Interior, among others. The program is only available on a Ministry of Forests computer in Victoria, so it is commonly used indirectly through TIPSY, which is a look-up and interpolation system that accesses yield tables generated by TASS (Di Lucca, 1998; Ministry of Forests and Range, 2009b). To illustrate model predictions, two examples were simulated on Scube and TIPSY, using site index 20: (a) A planted stand of pure spruce, unthinned, starting with 1000 stems per hectare at breast height. This density is near the upper end in the planted sample plots, but perhaps close to the minimum advisable operationally. (b) A natural stand with 80% spruce by basal area, and 2500 (spruce) stems per hectare at breast height, about average for the natural PSPs (Table 1). The mixed species facility in TIPSY actually applies to forest-level combinations of mono-specific stands, but it was used here as an approximation, specifying lodgepole pine for the other species component. TIPSY reports over-all totals per hectare, so it was assumed that 80% of the number of trees and volume, as well as basal area, was spruce.

Results are shown in Figure 8, superimposed on the PSP data. For the higher-density natural stand, both models agree closely in the basal area and total volume predictions. TIPSY predicts higher mortality and consequently larger tree sizes and higher merchantable volumes. For young plantations, TIPSY's predictions are below the observed basal areas, volumes, and dbh. Given the absence of data, predictions from both models for mature planted stands are speculative. VDYP-7 predictions generated with the program defaults were close to the lower boundary of the observed data (excluding the lowest plot, presumably damaged) and are not shown.

The time to reach breast height is highly variable, and in plantations it is sensitive to site preparation and to nursery and planting techniques. Estimates representing "typical" conditions are given by the Site Tools package (Ministry of Forests and Range, 2009a). According to it, at site index 20, age from seed is obtained by adding 13 and 9 years to breast-height age for natural and planted stands, respectively. See also Table 5 of Coates et al. (1994).

6. Discussion and Conclusions

The growth model is summarized in differential equation form in (20) and as invariants in the Summary of Projection Equations section. It may be surprising that such a simple model can describe basal area dynamics with only two free parameters (α and γ; ρ enters into the initialization). There is support for the observed relationships in the literature. It is sometimes thought that volume or biomass should follow an asymptotic sigmoid curve over time, and such an assumption is built into some yield tables. Tree physiologists have searched for plausible mechanisms to explain the implied growth rate decline after canopy closure (Ryan et al., 2004). Published volume-age trends for substantial bodies of data, however, are remarkably linear, at least within the main range of interest for management and considering mortality (Figure 11 in Sjolte-Jorgensen, 1967, Figure 4 in Pretzsch, 2005, García, 1990). This agrees with our initial finding of an age-independent gross BH increment (section Closed Stands, figure 2). Increment decreases slightly with spacing, which may induce some curvature when there is high mortality or repeated thinnings. The revised model (9)–(10) does imply a growth decline as H approaches its asymptote, but this occurs at advanced ages. The decrease in growth rate at wider spacings might be attributed to lower efficiency in utilizing space farther from the stem (García, 1990).

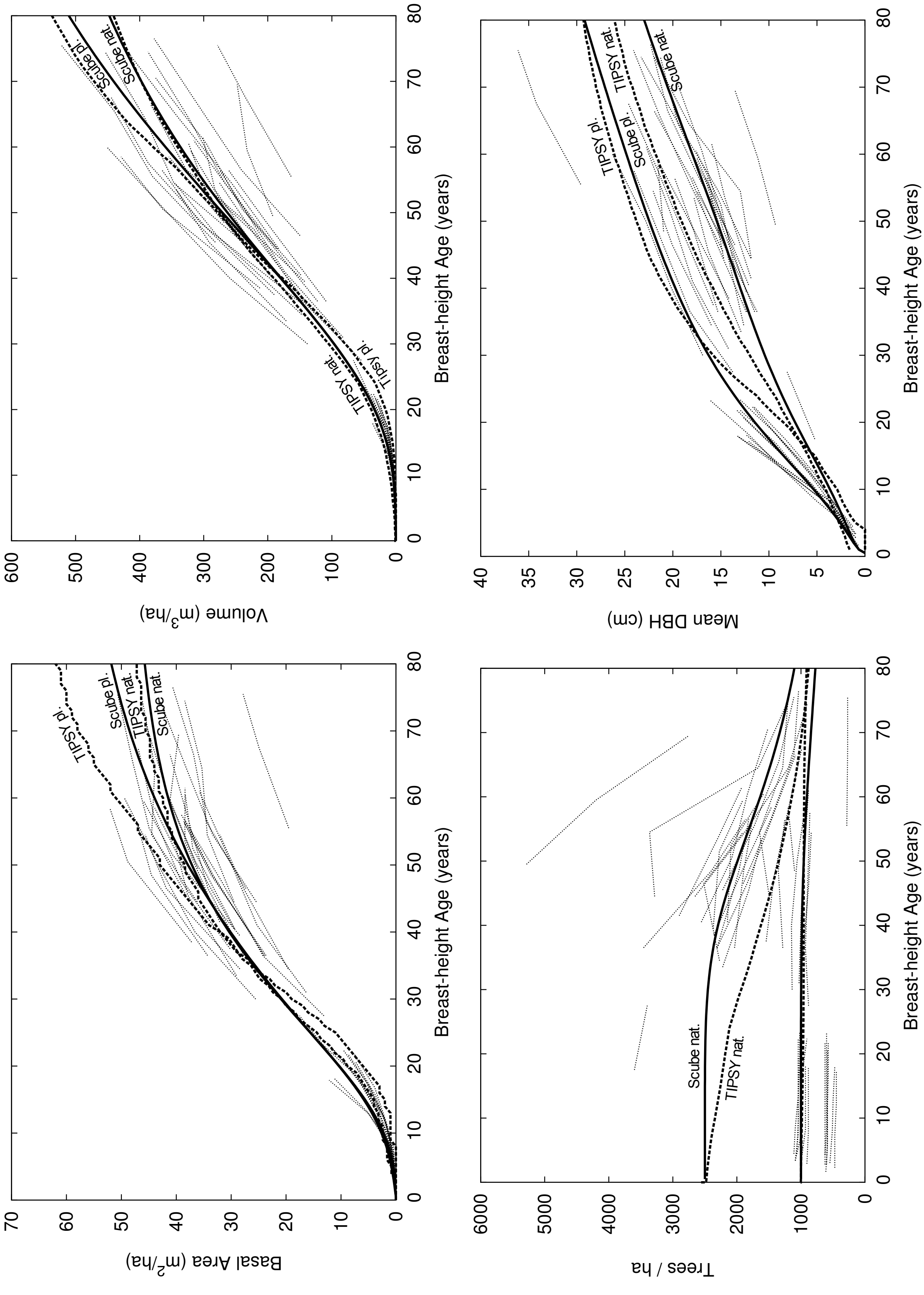

Figure 8: Data and predictions with Scube and TIPSY. Planted projections for pure spruce, with initial density of 1000 sph. Natural for 80% spruce, initial density 2500 sph.

Ignoring changes in N, (9)–(10) predicts that in closed canopy stands BH, and approximately volume per hectare, increase linearly with $H^{2-\beta}$, or as a quadratic in H if $\beta = 0$. For plantations where mortality is moderate, Alder (1980), Green et al. (1992), and Alder et al. (2003) have predicted volume per hectare with functions where the dominant term is a power of H with the estimated exponents being close to 2. If $\beta = 0$, dividing by H gives a relationship between B and H that tends to a straight line, as found by Beekhuis (1966), Hamilton and Christie (1971, Graphs 17–28), and Manley and Knowles (1980).

Closure and occupancy are in fact an abstraction and generalization of variables such as leaf area index (LAI), and intercepted photosynthetically active radiation (IPAR), commonly used in process models and ecophysiology. Relationships between IPAR and LAI, and between growth rates and IPAR, are presented by Balster and Marshall (2000), Allen et al. (2004), and Will et al. (2005), among others. For growth and yield prediction it is necessary, in addition, to model the dynamics of these variables in young stands, and as affected by thinning. In Scube, closure or occupancy are unobserved state variables, but in the future it may be possible to estimate them at an operational scale using remote sensing techniques, in particular LiDAR.

It should be interesting to evaluate the approach with more extensive data from other species. Complexity can be tailored to the information available: the more flexible variants with additional parameters may be used if warranted, or appropriate shape parameter values could be found and fixed for use in data-poor situations. The model can serve also as a parsimonious but biologically sound baseline where the scale parameters, as *multipliers*, may be further developed to include the effect of genetics (Carson et al., 1999), nutrients (García, 1989; Shula, 1989; Carlson et al., 2008), or climate (Landsberg and Waring, 1997; Woollons et al., 1997).

The modelling of dynamical systems through rates of change in continuous time, introduced by Isaac Newton, has for long been taken for granted in the physical sciences and engineering, and adopted more recently in some areas of biology (e.g., Lotka, 1924, Part II, Patten, 1971; Ford, 1999). There are few examples in forestry, however, an early one being Buckman (1962). It is more common to discretize time, typically in 5- or 10-year intervals, and use difference instead of differential equations. In simple instances the mathematics and computations are easier, but they become awkward when observation or projection intervals do not match the interval used in the model (McDill and Amateis, 1993; Weiskittel et al., 2007; Salas et al., 2008). Note that although Scube's variables are continuous, seasonal intra-annual growth fluctuations are not modelled.

An increasingly popular paradigm in forest growth and yield modelling makes a direct use of continuous transition functions. Sometimes called *algebraic difference equations* or *self-referencing functions*, these relationships are based on an invariant, not always made explicit, often motivated by a differential equation (Bailey and Clutter, 1974; Diéguez-Aranda et al., 2006; Tomé et al., 2006; Cieszewski and Strub, 2008). The present work generalizes that approach to more than one dependent variable and links it to mainstream dynamical systems theory. A rigorous mathematical foundation is provided by Arnold (1973, Ch. 1), who turns around the classical view by starting with families of smooth state trajectories ("flows") as the most primitive concept. It is shown that any flow can be described by a system of differential equations, although not all differential equations generate a flow. A flow is also determined by a complete set of independent first integrals, our invariants. First integrals may be defined in a more restrictive sense, in which "nonconstant first integrals are rarely encountered" (Arnold, 1973, page 77), so that the more generic terminology has been preferred here. Further discussion is contained in García (2011).

From a statistical point of view, it is interesting that different estimation methods produced similar parameter values and predictions, suggesting that an adequate representation of system dynamics might be insensitive to the details of stochastic modelling and statistical procedures.

Scube's modelling framework seems logically and biologically sound. The model describes well the available data, and its design makes extrapolations plausible. Considerable variability and uncertainty remains, however. These can only be resolved with proper long-term growth and yield monitoring, especially in second-growth planted stands.

Acknowledgements

Zhengjun Hu did much of the screening and data processing work, and developed an earlier preliminary model, as part of his Master of Science research at UNBC. The data was provided by the Forest Sciences Program Research Branch, and by the Forest Analysis and Inventory Branch of the British Columbia Ministry of Forests and Range. Useful comments from anonymous reviewers and the Associate Editor are gratefully acknowledged.

References

Alder, D., 1980. Forest volume estimation and yield prediction: Vol. 2 - Yield prediction. Forestry Paper 22/2, FAO, 194 pp.

Alder, D., Drichi, P., Elungat, D., 2003. Yields of Eucalyptus and Caribbean pine in Uganda. Consultancy report, Uganda Forest Resources Management and Conservation Programme Kampala, Uganda, 51 p.
URL `http://www.bio-met.co.uk/pdf/uymdoc.pdf`

Allen, C. B., Will, R. E., Sarigumba, T., Jacobson, M. A., Daniels, R. F., Kennerly, S. A., 2004. Relationship between canopy dynamics and stem volume production of four species receiving irrigation and fertilization. In: Connor, K. F. (Ed.), Proceedings of the 12th Biennial Southern Silvicultural Research Conference. General Technical Report. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC.

Arnold, V. I., 1973. Ordinary Differential Equations. The MIT Press, Cambridge, Massachusetts.

Bailey, R. L., Clutter, J. L., 1974. Base-age invariant polymorphic site curves. Forest Science 20, 155–159.

Balster, N. J., Marshall, J. D., 2000. Eight-year responses of light interception, effective leaf area index, and stemwood production in fertilized stands of interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca*). Canadian Journal of Forest Research 30, 733–743.

Bard, Y., 1974. Nonlinear Parameter Estimation. Academic Press, New York, 341 p.

Beekhuis, J., 1966. Prediction of yield and increment in *Pinus radiata* stands in New Zealand. Technical Paper 49, Forest Research Institute, NZ Forest Service.

Borders, B. E., Bailey, R. L., Clutter, M. L., 1988. Forest growth models: Parameter estimation using real growth series. In: Ek, A. R., Shifley, S. R., Burk, T. E. (Eds.), Forest Growth Modelling and Prediction. USDA Forest Service, General Technical Report NC-120, pp. 660–667.

Buckman, R., 1962. Growth and yield of red pine in Minnesota. Tech. Bull. 1272, US Department of Agriculture, 50 p.

Carlson, C. A., Fox, T. R., Lee Allen, H., Albaugh, T. J., 2008. Modeling mid-rotation fertilizer responses using the age-shift approach. Forest Ecology and Management 256 (3), 256–262.

Carson, S. D., Garcia, O., Hayes, J. D., 1999. Realized gain and prediction of yield with genetically improved *Pinus radiata* in New Zealand. Forest Science 45 (2), 186–200.

Cieszewski, C. J., Strub, M., 2008. Generalized algebraic difference approach derivation of dynamic site equations with polymorphism and variable asymptotes from exponential and logarithmic functions. Forest Science 54, 303–315.

Coates, K., Haeussler, S., Lindenburgh, S., Pojar, R., Stock, A., 1994. Ecology and silviculture of interior spruce in British Columbia. FRDA Report 220, Ministry of Forests, Forest Science Program.

Coopersmith, D., Mclellan, M., Stork, J., 1997. Experimental Project 660 — Overview of three experimental installations — A 30-year progress report. Research Note PG–12, British Columbia Forest Service, Forest Resources and Practices Team, Prince George Forest Region.
URL `http://www.for.gov.bc.ca/rni/Research/Extension_notes/PG12_EP660.pdf`

Di Lucca, C. M., 1998. TASS/SYLVER/TIPSY: systems for predicting the impact of silvicultural practices on yield, lumber value, economic return and other benefits. In: Bamsey, C. R. (Ed.), Stand Density Management Conference: Using the Planning Tools. November23–24, 1987, Edmonton, Alberta. Alberta Environmental Protection, pp. 7–16.

Diéguez-Aranda, U., Castedo Dorado, F., Álvarez González, J. G., Rojo Alboreca, A., Jan. 2006. Dynamic growth model for Scots pine (*Pinus sylvestris* L.) plantations in Galicia (north-western Spain). Ecological Modelling 191 (2), 225–242.

Ford, A., 1999. Modeling the Environment. Island Press, Washington, D. C., 401 p.

García, O., 1989. Growth modelling — new developments. In: Nagumo, H., Konohira, Y. (Eds.), Japan and New Zealand Symposium on Forestry Management Planning. Japan Association for Forestry Statistics, pp. 152–158.

García, O., 1990. Growth of thinned and pruned stands. In: James, R. N., Tarlton, G. L. (Eds.), New Approaches to Spacing and Thinning in Plantation Forestry: Proceedings of a IUFRO Symposium, Rotorua, New Zealand, 10–14 April 1989. Ministry of Forestry, FRI Bulletin No. 151, pp. 84–97.

García, O., 1994. The state-space approach in growth modelling. Canadian Journal of Forest Research 24, 1894–1903.

García, O., 2005. TADAM: A dynamic whole-stand approximation for the TASS growth model. The Forestry Chronicle 81 (4), 575–581, (Errata in For.Chron. 81: 815).

García, O., 2009. A simple and effective forest stand mortality model. International Journal of Mathematical and Computational Forestry & Natural-Resource Sciences (MCFNS) 1 (1), 1–9.

García, O., 2011. Dynamical implications of the variability representation in site-index modelling. European Journal of Forest Research 130 (4), 671–675.

García, O., Ruiz, F., 2003. A growth model for eucalypt in Galicia, Spain. Forest Ecology and Management 173, 49–62.

Goudie, J. W., 1998. Model validation: A search for the magic grove or the magic model. In: Bamsey, C. (Ed.), Stand density management: Planning and implementation. Edmonton, Alberta, pp. 45–58.

Goulding, C. J., 1979. Validation of growth models used in forest management. New Zealand Journal of Forestry 24 (1), 108–124.

Green, E. J., Strawderman, W. E., Thomas, C. E., 1992. Empirical Bayes development of Honduran pine yield models. Forest Science 38, 21–33.

Hale, S. E., 2003. The effect of thinning intensity on the below-canopy light environment in a Sitka spruce plantation. Forest Ecology and Management 179, 341–349.

Hamilton, G. J., Christie, J. M., 1971. Forest management tables (metric). Booklet 34, Forestry Commission, Her Majesty's Stationery Office, London, 201 pp.

Holten-Andersen, P., 1989. Danish yield tables in the past Century. Det Forstlige Forsogsvæsen i Danmark 42, 71–145.

Hu, Z., García, O., 2010. A height-growth and site-index model for interior spruce in the Sub-Boreal Spruce biogeoclimatic zone of British Columbia. Canadian Journal of Forest Research 40 (6), 1175–1183.

Husch, B., Beers, T. W., John A. Kershaw, J., 2003. Forest Mensuration, 4th Edition. Wiley, 443 p.

Landsberg, J., Waring, R., 1997. A generalized model of forest productivity using simplified concepts of radiation use efficiency, carbon balance and partitioning. Forest Ecology and Management 95, 209–228.

Lotka, A. J., 1924. Elements of Physical Biology. Williams and Wilkins Co., Inc., reprinted as *Elements of Mathematical Biology*, Dover, 1956. 465 p.

Manley, B. R., Knowles, R. L., 1980. Growth of radiata pine under the direct sawlog regime. New Zealand Journal of Forestry 25, 15–34.

McDill, M. E., Amateis, R. L., 1993. Fitting discrete-time dynamic models having any time interval. Forest Science 39, 499–519.

Meidinger, D., Pojar, J., February 1991. Ecosystems of British Columbia. Special Report Series 6, BC Ministry of Forests, Victoria, BC, Canada.

Ministry of Forests and Range, 2009a. Features of Site Tools, available online at `http://www.for.gov.bc.ca/hts/vdyp/`; last accessed July 2009.

Ministry of Forests and Range, 2009b. Tipsy Home Page, available online at `http://www.for.gov.bc.ca/hre/gymodels/TIPSY/`; last accessed July 2009.

Ministry of Forests and Range, 2009c. VDYP Home, available online at `http://www.for.gov.bc.ca/hts/vdyp/`; last accessed July 2009.

Mitchell, K. J., 1975. Dynamics and simulated yield of Douglas-fir. Forest Science Monograph 17, Society of American Foresters.

Mitchell, K. J., Cameron, I. R., May 1985. Managed stand yield tables for coastal Douglas-fir: Initial density and precommercial thinning. Land Management Report 31, B. C. Ministry of Forests, Research Branch, Victoria, British Columbia.

Mitchell, K. J., Stone, M., Grout, S. E., Di Lucca, C. M., Nigh, G., Goudie, J. W., Stone, J. N., Nussbaum, A. J., Stearns-Smith, A. Y. S., Brockley, R., 2004. TIPSY Version 3.2. B. C. Ministry of Forests, Research Branch, Victoria, B. C.

Nigh, G. D., 1995. Compatibility improvements and bias reduction in height-age models. Research Report 03, British Columbia Ministry of Forests, Research Branch, 10 p.

Patten, B. C., 1971. A primer for ecological modeling and simulation with analog and digital computers. In: Patten, B. C. (Ed.), Systems Analysis and Simulation in Ecology. Vol. 1. Academic Press, Ch. 1, pp. 3–120.

Pretzsch, H., 2005. Stand density and growth of Norway spruce (*Picea abies* (L.) Karst.) and European beech (*Fagus sylvatica* L.): evidence from long-term experimental plots. European Journal of Forest Research 124, 193–205.

R Development Core Team, 2009. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0.
URL `http://www.R-project.org`

Ryan, M. G., Binkley, D., Fownes, J. H., Senock, C. P. G. R. S., 2004. An experimental test of the causes of forest growth decline with stand age. Ecological Monographs 74 (3), 393–414.

Salas, C., Stage, A. R., Robinson, A. P., 2008. Modeling effects of overstory density and competing vegetation on tree height growth. Forest Science 54 (1), 107–122.

Seber, G. A. F., Wild, C. J., 2003. Nonlinear Regression. Wiley-Interscience, New York, 768 p.

Shula, R. G., 1989. CLAYSFERT: Stand growth model with P fertiliser effects for radiata pine on clay soil. FRI Bulletin 148, New Zealand Ministry of Forestry, Forest Research Institute.

Sjolte-Jorgensen, J., 1967. Influence of spacing on coniferous plantations. In: Romberger, J. A., Mikola, P. (Eds.), International Review of Forestry Research. Vol. 2. Academic Press, New York, pp. 43–94.

Tomé, J., Tomé, M., Barreiro, S., Paulo, J. A., 2006. Age-independent difference equations for modelling tree and stand growth. Canadian Journal of Forest Research 36, 1621–1630.

van Laar, A., Akça, A., 2007. Forest Mensuration, 2nd Edition. Springer.

Vanclay, J., Skovsgaard, J., 1997. Evaluating forest growth models. Ecological Modelling 98, 1–12.

Venables, W. N., Ripley, B. D., 2002. Modern Applied Statistics with S, 4th Edition. Springer, New York, 495 p.

von Gadow, K., Hui, G., 1999. Modelling Forest Development. Vol. 57 of Forestry Sciences. Kluwer Academic Publishers, Dordrecht, Te Netherlands, 213 p.

Walton, A., May 2009. Provincial-level projection of the current mountain pine beetle outbreak: Update of the infestation projection based on the 2008 provincial aerial overview of forest health and revisions to the “Model” (BCMPB.v6). Tech. rep., Research Branch, BC Forest Service.

Weiskittel, A. R., Garber, S. M., Johnson, G. P., Maguire, D. A., Monserud, R. A., Oct. 2007. Annualized diameter and height growth equations for Pacific Northwest plantation-grown Douglas-fir, western hemlock, and red alder. Forest Ecology and Management 250 (3), 266–278.

Will, R. E., Narahari, N. V., Shiver, B. D., O.Teskey, R., 2005. Effects of planting density on canopy dynamics and stem growth for intensively managed loblolly pine stands. Forest Ecology and Management 205 (1-3), 29–41.

Woollons, R., Snowdon, P., Mitchell, N., 1997. Augmenting empirical stand projection equations with edaphic and climate variables. Forest Ecology and Management 98, 267–274.

Xie, C.-Y., Yanchuk, A., Kiss, G., 1998. Genetics of interior spruce in British Columbia: performance and variability of open-pollinated families in the East Kootenays. Research Report 07, BC Ministry of Forests, Research Program.