Building a dynamic growth model for trembling aspen in Western Canada without age data

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Abstract:

A biologically-inspired whole-stand growth and yield model was developed for even-aged thinned or unthinned stands dominated by trembling aspen. Estimation used permanent sample plot data from British Columbia, Alberta, Saskatchewan and Manitoba, supplemented by published site index and young stand information. An ingrowth imputation procedure was devised to facilitate the use of plot measurements where small trees are not measured. Two published site index models were closely approximated by a simple age-base invariant equation. Good parameter estimates for mortality and basal area growth were obtained without using age observations, which were unreliable or missing. Four differential equations describe the dynamics of top height, trees per hectare, basal area, and a site occupancy factor. Current values of these variables are used to estimate total and merchantable volumes up to any diameter limit, and diameter distribution parameters. When an independent source of site quality estimates is available, the final model does not require stand age knowledge for making growth and yield predictions.

Key words: Forest growth and yield, *Populus tremuloides*, quacking aspen, thinning, dynamical systems, *TAG*.

1. Introduction

Trembling or quaking aspen (*Populus tremuloides* Michx.) is the most widely distributed tree in North America (Perala, 1990). In recent years it has gone from being considered a weed species, to becoming an increasingly important source of wood for oriented strand-board, pulp, lumber, and veneer (Penner *et al.*, 2001; Nigh *et al.*, 2002; Domke *et al.*, 2008). According to Peterson and Peterson (1996), the main zone of commercial potential for aspen forest products in Canada extends from north-eastern British Columbia to south-eastern Manitoba, although there is renewed interest in aspen utilization in Ontario (Rice *et al.*, 2001; Penner *et al.*, 2001), Quebec (Fortier *et al.*, 2012), and the north-central United States (Perala *et al.*, 1999; Domke *et al.*, 2008).

I describe a whole-stand growth model (named *TAG*, for Trembling Aspen Growth) capable of projecting growth and yield of aspen-dominated unthinned or thinned stands. Data came from an extensive database contributed by agencies from British Columbia, Alberta, Saskatchewan and Manitoba, previously used in the aspen version of the STIM model (de Jong *et al.*, 1996; Flewelling *et al.*, 1996). These permanent sample plot data were supplemented by published site index and young stand development information. An ingrowth estimation procedure made available early growth data that had been ex-

cluded in STIM. The basic model is similar to the ones for white spruce and loblolly pine of García (2011) and García *et al.* (2011). However, a simplifying assumption that avoided numerical integration in those models was found to be unsatisfactory, possibly because of the aspen much wider range of initial densities and lower shade tolerance. Another innovation was the exclusion of age information from the final model fitting, avoiding the unreliable ages that are a weakness of the database (Flewelling *et al.*, 1996). Given independent site quality estimates (e.g., Mah and Nigh, 2003), ages are not required either for applying the model, which is important because in inventories ages are often unavailable or inaccurate (Magnussen and Russo, 2012).

The plan of the article is as follows. Data sources and processing are discussed first. The data represent stands with more than 70% aspen by basal area, originating from root sucker regeneration following harvesting or fire. Under conditions that are not well understood, mature aspen can suffer catastrophic mortality leading to stand succession (Frey *et al.*, 2004; Pothier *et al.*, 2004; Meng *et al.*, 2008). This process is outside the scope of the model and some plots exhibiting such break-up were excluded.

The analysis and results are then presented separately for the three main model components, height, mortality and basal area. Top height growth is based mainly on published site index models. The mortality sub-model combines permanent sample plots, and published early mortality observations that are poorly represented in the database.

Basal area growth is modelled through increments of the product of basal area and top height, a proxy for stand volume or biomass. Gross increment in closed-canopy stands is modified by an *occupancy* factor that represents the reduced capture of site resources in more open young or recently thinned

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stands. Occupancy is related to initial density, it increases over time, and is reduced by thinning. Mortality, and growth in basal area and occupancy, are expressed relative to height increment, providing for age independence. The article ends with a discussion and conclusions.

The use of the model also requires auxilliary relationships such as total and merchantable stand volume equations, and optionally diameter distributions and relationships between basal area and number of trees removed in thinnings. Since these are not the focus of the study, they are provided as *Supplementary Material* in the Journal web site. That material includes also additional result details. Model implementations can be downloaded from `http://forestgrowth.unbc.ca/tag`, together with a report containing further model development details and computer code.

2. Data

2.1. Permanent plot data base

The permanent sample plot data had been used in the aspen STIM model (de Jong *et al.*, 1996), and were obtained from the Pacific Forestry Centre of the Canadian Forest Service. The data originated from agencies throughout Western Canada: Alberta Forest Service (Alberta), British Columbia Ministry of Forests (British Columbia), Canadian Forest Service (Manitoba and Saskatchewan), Saskatchewan Environment and Resource Management (Saskatchewan), Weldwood Canada Ltd. (Alberta), and Weyerhaeuser Canada (Alberta). STIM also used US Forest Service plots from the North-Central United States that were excluded from the model described here, although some of the data were used in thinning relationships (*Supplementary Material*). The extensive database for aspen, spruce, and aspen-spruce mixedwoods (including smaller proportions of other species) was initially compiled and depurated by Nemec (1994), and the aspen-dominated even-aged plots were processed further by Paul Boudewyn and others for use in STIM (Flewelling *et al.*, 1996). For this model, additional calculations and data screening were performed as follows.

2.1.1. Age calculation

Models including age were evaluated, although later discarded. The majority of the measurements had only total age estimates provided by the data owners in header records. Some plots had growth-ring counts at breast height or at stump height, while others had no age information. The origin of the owner-provided ages is uncertain, and sometimes differed considerably from those derived from ring counts for the same plots.

Ring counts were preferred to owner ages where available for 3 or more trees in a plot. If necessary, these were harmonized to be consistent with the known measurement dates. Site indices and breast-height ages were calculated with an iterative procedure based on the site-index model of Section 3.1. These values were not used in the final model, so we omit the details.

Breast-height age was defined as number of growth rings at breast height, implying a height of 1.3 m at an age of 0.5 years (Haddon, 1988; Nigh, 1995; Hu and García, 2010).

2.1.2. Top height calculation

Stand top height was defined as the height of the largest-diameter suitable aspen tree in 0.01 hectares (Forest Productivity Council, 1988). To correct for selection bias in plots of area $A > 0.01$ hectares, top height was calculated as the mean of the $160A - 0.6$ largest aspen trees, interpolating linearly between the nearest integers (García, 1998; García and Batho, 2005). This method was preferred to the theoretically less biased U-estimator because it is less affected by missing or inaccurate small tree measurements.

All tree heights were obtained from the nonlinear height-diameter regression of Martin and Flewelling (1998) fitted to height sample trees in each plot measurement. Only measurements with at least 5 aspen height sample trees were used, and a few plot measurements with erratic height-diameter observations were excluded.

2.1.3. Ingrowth

Trees were most often measured only above dbh thresholds of 5.1, 7.1, 7.5, or 9.1 cm, varying across data sources. Subplots for smaller trees existed in a few instances, but these were generally small, and the information imprecise and difficult to use (Flewelling, 1981; Flewelling *et al.*, 1996). The problem was solved in STIM by excluding all trees smaller than 9.1 cm. Unfortunately, that drastically reduced the number of measurement in young stands, limiting predictions to top heights above 12 m, and required a somewhat cumbersome and unreliable separate ingrowth sub-model (de Jong *et al.*, 1996; Flewelling *et al.*, 1996). For this model it was decided instead to estimate the number and basal area of the unmeasured trees whenever the potential error was not too high.

Trees in the permanent sample plots had been identified with numbered tags. The number of trees in a plot at any measurement was estimated by adding any new trees that appeared in future measurements. This might ignore trees that die before reaching the dbh threshold, and possibly include regeneration appearing after the measurement, but the net effect of such differences should be small.

The dbh for a missing tree that appears in a later measurement was estimated through a ratio estimator, as the product of the later dbh and the ratio between the dbh sum in the current measurement and the dbh sum in the later measurement, summing over the trees present in both measurements. If this was greater than the dbh threshold, the threshold was substituted. The basal areas thus obtained were used only if the estimated basal area ingrowth was less than 10% of the total.

2.1.4. Species composition filtering

The original database was compiled with a view to studying trembling aspen and white spruce mixtures. Many plots contain also substantial proportions of other conifers and hardwoods. The observations where aspen was dominant were selected for this model. These were defined as those measurements where currently and at any time in the past aspen constituted at least 70% of the basal area, and was not surpassed in top height by any other species group. Similar criteria were used by Flewelling *et al.* (1996).

2.1.5. Stand breakup

Aspen often suffers sudden mortality and breakup processes that can destroy the stand in a short period of time; the causes
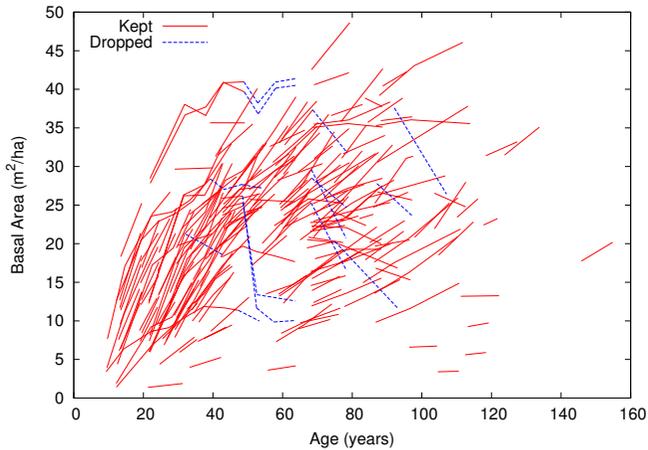
Fig. 1. Mortality events with basal area decreasing more than 1% per year were excluded, as well as later measurements in the same plot (dashed lines). These likely represent stand breakup, or possibly catastrophic storm or pest damage, not contemplated in the model predictions. Growth periods with unknown ages are not shown.

are poorly understood (Frey *et al.*, 2004). Increased propensity to breakup may exhibit regional differences, that have been associated with poor sites (Carmean *et al.*, 2006) or with warmer climates (Perala *et al.*, 1996). Breakup is rare in north-eastern British Columbia, where aspen trees tend to remain healthy and reach large dimensions (Kabzems and García, 2004).

Flewelling *et al.* (1996) note that "our data base is lacking evidence of severe declines". However, graphs such as Figure 1 show periods of heavy mortality, at least some of them likely due to breakup. Some may reflect extreme effects of drought or pests (Hogg *et al.*, 2008), or catastrophic storm damage. Other cases may not appear in the data because after the event the plots may have been abandoned, or aspen may have ceased to be dominant.

Predicting such extreme events is outside the scope of the growth model, they should be taken into account separately as risks when evaluating management decisions. Moderate mortality and "normal" observation error should be kept, however, to prevent bias. From graphs it appeared that a 1% decrease in basal area per year (over the typically 5- to 15-year measurement intervals) might be a reasonable threshold to separate both kinds of mortality; periods above this limit were removed (Figure 1). Later measurements in the same plot were also excluded.

The presumed breakup appears largely unrelated to age or other stand variables, except that it occurs normally at top heights of 20 m or more.

2.1.6. Additional screening

The data were examined graphically for gross observation or transcription errors, leading to the removal of a few measurements. A few measurements were omitted also where dead trees were much larger than the average survivor (high k-values, Section 3.2.3), suggesting an uneven-aged structure.

The data coverage can be appreciated in Figures 1, 2, 4, and 5. Table 1 shows statistics for the growth intervals used in the

final basal area sub-model. These values exclude the 197 intervals from breast height to the initial plot measurement. For mortality, additional measurements where the estimated basal area ingrowth exceeded 10% were used, totalling 392 intervals from 236 plots.

2.2. Published young stand data

Data for very young stands was not available in the permanent sample plot database. Therefore, for height growth before breast height (Section 3.1.2), and for mortality (Section 3.2), the plot data was supplemented by height and stand density measurements obtained from the literature. Useful data were extracted from Bella (1986, based on the experiments of Bella and DeFranceschi (1972)), Perala (1984), Sorensen (1968), Strothmann and Heinselman (1957), and Weingartner (1980). Other data sources listed by Peterson and Peterson (1996) reproduce some of this same data.

Most height values in these data were plot means, and a stand top height was approximated multiplying by $1 + 0.05 \ln(N/100)$, where N is number of trees per hectare. This factor was derived from young permanent sample plots, and from published data where both height measures were available.

3. Growth analysis and results

Development of the height growth, mortality and basal area growth components will be described in turn. Each of these consist of a differential equation that is integrated to specify a transition between any two points in time (García, 1994). The equation forms follow closely those of García (2011) and García *et al.* (2011).

3.1. Height and site

3.1.1. Top height growth and site index model

The height growth sub-model was derived from two studies supported by extensive stem-analysis databases. Nigh *et al.* (2002) obtained separate and combined site index models for 6 biogeoclimatic zones in British Columbia, based on nonlinear least-squares fitting of a growth function equivalent to the Hossfeld IV in the terminology of Zeide (1993) and García (2008). Carmean *et al.* (2006) used nonlinear least-squares methods and a variant of the Bertalanffy-Richards function with three regional data sets from north-western Ontario.

Top height predictions from the published models were computed for ages 5, 10, ..., 120 years, and site indices 5, 10, ..., 30 (meters at breast-height age 50). The points from Carmean *et al.* (2006) were shifted 0.5 years to the right to match the breast-height age definition used here (Section 2.1.1). Both models are very similar over the whole range of ages and sites. A good base-age-invariant approximation to the model predictions was obtained as a family of monomolecular or Mitscherlich growth curves (Zeide, 1993; García, 2008) parametrized by a site quality parameter q, fitted with the *EasySDE* package (`http://forestgrowth.unbc.ca/sde`) (Figure 2). The permanent sample plot data is shown for comparison.

Table 1. Permanent sample plot data for the basal area sub-model. 352 growth intervals from 197 plots.

|	Mean	SD	Minimum	Quartile 1	Median	Quartile 3	Maximum
Plot size (ha)	0.07771	0.01265	0.04050	0.08067	0.08090	0.08090	0.10120
Aspen %	0.9121	0.0958	0.7029	0.8336	0.9513	1.0000	1.0000
Measurement interval (yr)	8.324	3.388	2.000	6.000	8.000	10.000	26.000
1st year	1968	9.326	1948	1961	1969	1977	1987
2nd year	1977	9.946	1953	1969	1978	1986	1992
1st top height (m)	17.45	4.77	4.11	14.13	17.96	20.94	27.72
2nd top height (m)	19.26	4.57	5.81	16.74	19.65	22.65	29.32
1st density (trees/ha)	1352	1415	162	655	915	1524	14518
2nd density (trees/ha)	1166	1022	162	598	840	1383	8442
1st basal area (m^2/ha)	20.58	8.75	1.38	13.54	20.92	25.93	43.05
2nd basal area (m^2/ha)	23.89	8.57	1.89	17.90	23.98	29.34	48.62
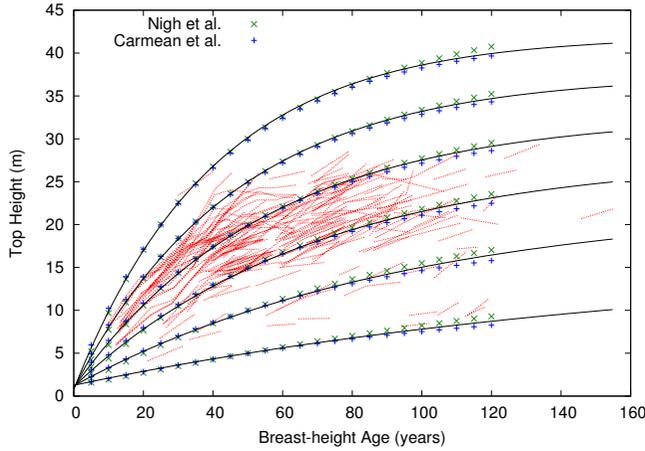
Fig. 2. Top height over breast-height age. Points calculated with the combined model of Nigh *et al.* (2002) and the model of Carmean *et al.* (2006, adjusting for the different age definitions). Dotted lines show the permanent sample plot data. Solid curves are from the fitted model for site indices 5, 10, ..., 30.

The fitted model corresponds to the differential equation

$$[1] \qquad \frac{\mathrm{d}H}{\mathrm{d}t} = q(8.568 + 1342q - H) ,$$

where H is top height in metres, t is time in years, and q is the site-dependent parameter. Integration gives the transition function

$$[2] \qquad H_2 = 8.568 + 1342q - (8.568 + 1342q - H_1)\mathrm{e}^{-q(t_2-t_1)}$$

that relates predictions at any two points (t_1, H_1) and (t_2, H_2). Site index curves are obtained by substituting the origin $t_1 = 0.5$, $H_1 = 1.3$.

The conventional site index (base age 50) is related to q by

$$[3] \qquad S = 8.568 + 1342q - (7.268 + 1342q)\mathrm{e}^{-49.5q} .$$

This equation must be solved numerically to obtain q for a given S.

Site index curves calculated from this model differ from those of Nigh *et al.* (2002) and Carmean *et al.* (2006) by no more than 0.5 m for ages 0–100 years and site indices 5–30.

Incorporating the permanent sample plot data did not change much the parameter estimates, indicating compatibility between the model and the plot data. The estimates based only on the published models were adopted, considering their support and the uncertainty about the plot age observations.

Another site index model was developed by Huang *et al.* (2009) for aspen growth modelling in Alberta. The curves are similar to ours for low and medium site indices, but differ at high site qualities; there is no detailed information on the data and methods used. Nigh *et al.* (2002) included an adequate sample of stands around site index 30 that support the current model (Gordon Nigh, pers. comm., August 2011).

Site quality parameters q based on the model of equation [1] were estimated with *EasySDE* for all plots that had age observations. These were needed for the height increment smoothing described below, but after evaluation the approach was not used in the final model.

3.1.2. Years to breast height

In addition to breast-height age, it is useful to have predictions based on total age. The transition function [2] could be extrapolated to $t_1 = 0$, $H_1 = 0$, as in Huang *et al.* (2009). However, aspen sucker regeneration is known to grow very rapidly during the first growing season, presumably taking advantage of an established root system and stored carbohydrates (Perala *et al.*, 1996; Peterson and Peterson, 1996). Therefore, we allow the first-year increment to deviate from the growth curve, estimating an age displacement T_0 at height $H = 0$:

$$[4] \qquad H = (8.568 + 1342q)[1 - \mathrm{e}^{-q(T+T_0)}] ,$$

where T is total age, counted from stand initiation at harvesting or fire.

The new parameter was estimated as $T_0 = 0.6829$, using *EasySDE* and published young stand data described in Section 2.2 (Figure 3). From [2] and [4], the estimated difference between total age T and breast-height age A is

$$[5] \qquad T - A = -\ln(1 - \frac{1.3}{8.568 + 1342q})/q - 1.183 .$$

3.1.3. Smoothing height increments

Mortality and basal area increments were modelled relative to the top height growth between consecutive measurements. Top height observations are subject to considerable sampling and measurement error, causing height increments to be highly variable. To reduce this variability, García (2011) and García *et al.* (2011) substituted the prediction from the height model
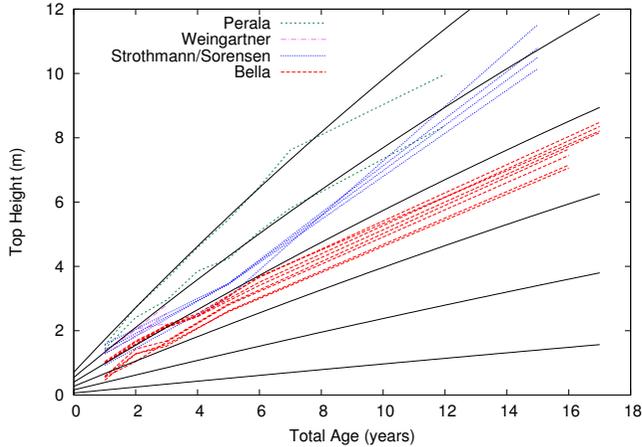
Fig. 3. Total-age site curves, and published young stand height-age data. Site indices 5, 10, ..., 30.
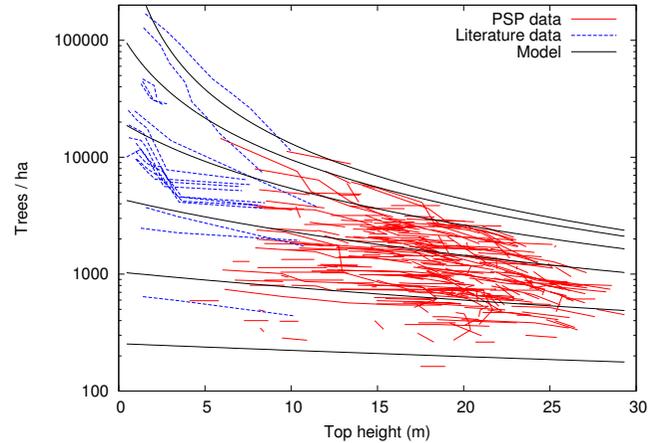

Fig. 4. Mortality data, with stand density for all species graphed on a logarithmic scale. Heights are raw, non-smoothed observations. Some model projections are also shown.

transition function for the second height in each pair of consecutive measurements.

A similar but more symmetric approach was tested here, substituting estimates $\hat{H}_1$ and $\hat{H}_2$ for both heights. The estimates minimize the sum of squares

$$(H_1 - \hat{H}_1)^2 + (H_2 - \hat{H}_2)^2 ,$$

subject to satisfying Equation [2], i. e.,

$$\hat{H}_2 = a - (a - \hat{H}_1)e^{-q\Delta t} ,$$

where $a = 8.568 + 1342q$. The method of Lagrange multipliers gives the estimates

$$\hat{H}_1 = a - \frac{a - H_1 + (a - H_2)e^{-q\Delta t}}{1 + e^{-2q\Delta t}} ,$$
$$\hat{H}_2 = a - (a - \hat{H}_1)e^{-q\Delta t} .$$

Although observation noise is much reduced, this smoothing depends on the uncertain age information through the site quality estimates (c.f. Sections 2.1.1 and 3.1.1), and plots without age have to be excluded. The alternative was to use only the raw height data H_1, H_2.

3.2. Mortality

3.2.1. Decrease in number of trees

Aspen root suckering usually produces high initial stand densities, that are quickly reduced by heavy competition-induced mortality (Peterson and Peterson, 1996; Perala *et al.*, 1999). The permanent sample plot data do not cover those early years. Therefore, to develop a more representative mortality model the plot data were pooled with observations from young stands extracted from the literature as described in Section 2.2 (Figure 4).

The rate of mortality relative to top height growth was modelled as

$$[6] \qquad \frac{dN_T}{dH} = -a_1 H^{a_2} N_T^{a_3} ,$$

Table 2. Parameter estimates and residual standard errors for the mortality regression

	n	a_1	a_2	a_3	RSE
Raw heights	392	0.0004561	0	1.616	0.1374
Smoothed heights	356	0.0005303	0	1.600	0.1321

where N_T is the all-species total number of stems per hectare, and a_1, a_2 and a_3 are parameters to be estimated. Integrating equation [6] one obtains the following equation for consecutive measurements (H_1, N_{T1}) and (H_2, N_{T2}):

$$[7] \qquad \ln N_{T2} = \ln[N_{T1}^{1-a_3} + a_1 \frac{a_3 - 1}{a_2 + 1}(H_2^{a_2+1} - H_1^{a_2+1})]$$
$$/(1 - a_3) ,$$

from which the parameters were estimated by nonlinear least-squares regression. Both raw and smoothed heights (Section 3.1.3) were tried. In both instances, a_2 was found to be non-significant, so it was fixed at 0 (see *Supplementary Material*). Results are given in Table 2 and Figure 4.

The standard errors were similar, in part because the larger available sample size compensated for the higher variability of the raw values. There may be some risk of bias from the smoothing based on unreliable site estimates. The parameter estimates from the raw data were used.

3.2.2. Species composition

The stand density N_T in the previous Section is for all species, but the growth model uses values for the aspen component. Knowing the number N of aspen per hectare and the proportion p_N of aspen (by number), $N_T = N/p_N$ can be substituted for N in equations [6] and [7]. However, usually species composition is better specified as a proportion (or percentage) of basal area, because this tends to be more stable and biologically relevant.

García (2011) and García *et al.* (2011) found in interior spruce and in loblolly pine, respectively, that the proportion of the dominant species by number of trees was approximately

$p_N = p^2$, where p is the proportion by basal area, reflecting the substantially larger diameters of the dominant species. In contrast, plotting the aspen-spruce data showed little systematic deviation from a direct relationship. For the aspen-dominated stands ($p \geq 0.7$), approximately,

[8] $p_N = p^{1.12}$.

Hence, Equation [6] becomes

[9] $\dfrac{dN}{dH} = -a_1 p^{1.12(1-a_3)} H^{a_2} N^{a_3}$,

and, assuming a constant p, the transition function is

[10] $N_2 = [N_1^{1-a_3} + a_1 \dfrac{a_3 - 1}{a_2 + 1} p^{1.12(1-a_3)} (H_2^{a_2+1} - H_1^{a_2+1})]^{1/(1-a_3)}$.

Any effects of changes in p between consecutive measurements are neglected. In our data there was no evidence of decreasing or increasing trends in species composition, after removing cases of stand breakup (Section 2.1.5). Meng *et al.* (2008) found declines in p for mature stands in Alberta. Modelling such species dynamics is not attempted here, although the final model is capable of simulating externally given composition changes.

3.2.3. Basal area mortality

The model also needs an estimate of the mortality in terms of basal area per hectare (B), or in terms of the product of basal area and top height. Mortality in $W = BH$ equals the mortality in number of trees, $-dN/dH$, times the mean tree size W/N, times a factor k that represents the size of dead trees relative to that of the survivors. Observed k-values are extremely variable, but a precise estimate is not critical (García, 2011). The aforementioned data screening already excluded a few plots with $k > 2$ because they were suspected to be uneven-aged.

Various methods gave estimates of k between 0.47 and 0.63 (see the report at http://forestgrowth.unbc.ca/tag and García (2011) for details). The presence of mortality due to causes other than suppression may cause some overestimation. Values of 0.5 and 0.6 were tried in the basal area growth model, with $k = 0.5$ giving the best results.

3.3. Basal area

I modelled the growth of the product of aspen basal area (m²/ha) and top height, $W = BH$, rather than basal area growth directly. W is approximately linearly related to volume and biomass, and leads to simpler biologically-based equations. Growth was formulated relative to top height growth, assumed to be independent of site quality. Examination of the model residuals confirmed that this assumption was satisfactory.

The increment can be partitioned into two components:

[11] $\dfrac{dW}{dH} = \text{gross increment} - \text{mortality}$.

From Section 3.2.3, the second term on the right-hand side is

$\text{mortality} = -k \dfrac{W}{N} \dfrac{dN}{dH}$.

3.3.1. Gross increment

For closed-canopy stands, the gross increment depends on the current stand height and density. Basal area or diameter were not included as predictors because the biological relevance of the amount of wood accumulated on the stems seems doubtful (García, 2011). A sufficiently flexible formulation that excludes negative predictions is $b_1 p H^{b_2} N^{b_3}$, where p is the proportion of aspen (Section 3.2.2) and the b_i are parameters to be estimated. Young stands, and stands shortly following thinning or other disturbances, have not reached or recovered full canopy closure, and do not make full use of the site potential. Growth is then reduced by a factor Ω that represents site occupancy relative to that in a fully closed stand:

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

with $\Omega = 1$ for closed stands. In this model the *occupancy* Ω is an unobserved proxy for above- and below-ground resource capture; it was estimated indirectly from the stand dynamics.

Substituting in [11], the rate equation for W becomes

[12] $\dfrac{dW}{dH} = b_1 p \Omega H^{b_2} N^{b_3} + k \dfrac{W}{N} \dfrac{dN}{dH}$.

3.3.2. Occupancy

To complete the system dynamics description, an equation for the rate of change in Ω is needed. A simple model has been found satisfactory, where at low occupancy levels the rate depends on H in the same way as the gross increment, decreasing linearly down to an asymptotic equilibrium at $\Omega = 1$:

[13] $\dfrac{d\Omega}{dH} = c_1 p H (1 - \Omega)$.

Integration gives

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

From [12] and [13], it can be verified by differentiation that the transition equation for W is then

[15] $W_2 = N_2^k [W_1/N_1^k + b_1 p \int_{H_1}^{H_2} \Omega N^{b_3-k} H^{b_2}\, dH]$.

Inside the integral, N and Ω are given as functions of H by [10] and [14] (dropping the subscript 2 in those equations). García (2011) and García *et al.* (2011) found that the special case $b_3 = k$ was satisfactory, resulting in a simple explicit form for [15]. Both alternatives $b_3 = k$ and $b_3 \neq k$ were tested here.

3.3.3. Initialization

Starting from given values of H_1, N_1, W_1 and Ω_1, equations [2], [10], [14] and [15] predict the state of the stand $t_2 - t_1$ years later. If the stand is known to be near full closure, Ω_1 can be taken as 1, otherwise an initial estimate is needed. For that purpose, another unobserved variable was included in the model, the *relative closure* R.

R represents an amount of foliage and fine roots, the "resource capture apparatus", relative to that in a fully closed stand. The resources captured, Ω, are non-linearly related to R, increasing proportionally to R when R is small, and tending to

a horizontal asymptote when R approaches 1. The exact relationship is not critical for the model predictions, and following previous work it was assumed to be

[16] $\Omega = 1 - (1 - R)^{2.6}$.

The exponent 2.6 was found to give a slightly better basal area fit than the 2.2 for spruce of García (2011), and the 2.4 for loblolly pine of García *et al.* (2011). The curve is very close to one obtained for radiata pine in New Zealand, using a different equation (García, 2011).

On thinning, it is assumed that R decreases proportionally to the basal area removed. With the subscripts 1 and 2 indicating before and after thinning, respectively,

[17] $R_2 = (B_2/B_1)R_1$.

The change in Ω is obtained using Equation [16].

Bare-land predictions are conveniently initialized at breast-height, with $H = 1.3$, $N = N_0$ assumed known or back-projected with [10], $B = 0$, and R proportional to the number of trees:

[18] $R_0 = \max\{N_0/c_2, 1\}$.

The parameter c_2 can be interpreted as the number of trees needed for full closure at breast height.

In more complex situations, Ω can be projected through repeated application of equations [10], [18], [16], [14], and [17].

3.3.4. Parameter estimation

The parameters $b_1, b_2, b_3, c_1,$ and c_2 were estimated by minimizing the root mean squared error (RMSE) of the basal area predictions $B_2 = W_2/H_2$, with W_2 given by [15]. An initial breast-height point was included for each plot, initialized as described in Section 3.3.3. Two ways of calculating the predictions were tried, one starting from the breast-height point, and the other starting from the preceding observation (shortest interval). In both cases, inverse time-interval weighting was also tried, giving the four estimation methods described by García (2011). In addition, predictions were calculated using either raw observed top heights, or the smoother height estimates of Section 3.1.3.

The RMSE was minimized with a general-purpose optimization algorithm (function *optim*, R Development Core Team, 2009). The integral in [15] was approximated by adaptive quadrature with the R function *integrate*. In each instance, several runs with starting points obtained from nonlinear regression on closed-canopy stands or from other model variants were used, to guard against local optima. Model variants and estimation criteria were evaluated based on the RMSE, residual plotting, and/or parsimony. Methods are described in more detail by García (2011) and García *et al.* (2011).

Unlike in previous work, fixing $b_3 = k$ was unsatisfactory, causing over-estimation in young stands at high densities, and under-estimation at low densities. In common with those studies, $b_2 = 1$ was nearly optimum, and time-interval weighting had little effect. The value $k = 0.5$ gave better fits than $k = 0.6$.

Results for the two prediction interval types (no weighting), and for raw and smoothed heights, are given in Table 3. The
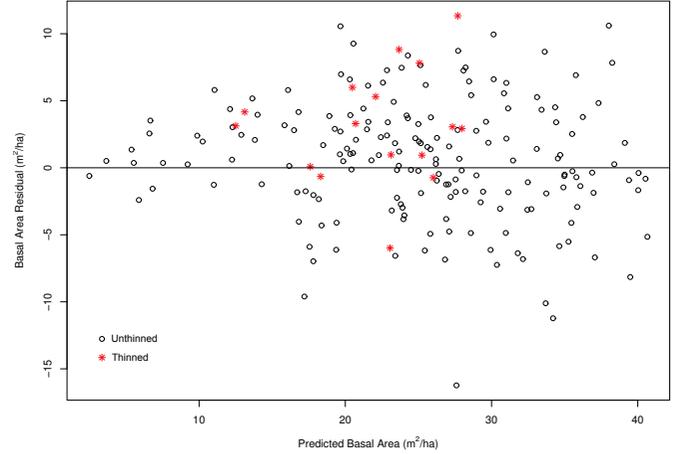

Fig. 5. Basal area residuals (observed minus predicted) for predictions starting from breast height.

prediction intervals starting at breast height were longer than the intervals between consecutive measurements, and therefore the RMSE are not comparable. However, the residual graphs were practically indistinguishable. Height smoothing reduces the variability of the residuals, although it is not clear if that should improve the estimates. In this instance, as in Section 3.2.1, the difference in number of observations due to missing ages compensated for the variability, causing the RMSE to be similar. Considering the potential for bias arising from the unreliable age data, the raw-height estimates were chosen, specifically, those on the third row of Table 3.

Plots of prediction residuals over the various stand variables were satisfactory, showing no obvious patterns (e.g., Figure 5). In particular, there was no trend with site quality, supporting the use of site-independent growth relative to height increment. Additional graphs and fit statistics are shown in the *Supplementary Material*.

3.4. Growth equations summary

Substituting the parameter estimates, the differential equation system defining the model is

[19a] $\dfrac{\mathrm{d}H}{\mathrm{d}t} = q(8.568 + 1342q - H)$

[19b] $\dfrac{\mathrm{d}N}{\mathrm{d}H} = -0.0004561p^{-0.6898}N^{1.616}$

[19c] $\dfrac{\mathrm{d}\Omega}{\mathrm{d}H} = 0.01023pH(1 - \Omega)$

[19d] $\dfrac{\mathrm{d}W}{\mathrm{d}H} = 2.018p\Omega HN^{0.06518} + 0.5\dfrac{W}{N}\dfrac{\mathrm{d}N}{\mathrm{d}H}$

Given the state of the stand at time t_1, the following transition equations can be solved sequentially to predict the state at time t_2:

[20a] $H_2 = 8.568 + 1342q - (8.568 + 1342q - H_1)\mathrm{e}^{-q(t_2-t_1)}$

[20b] $N_2 = [N_1^{-0.6159} + 0.000280912p^{-0.6898}(H_2 - H_1)]^{-1/0.6159}$

[20c] $\Omega_2 = 1 - (1 - \Omega_1)\exp[-0.005115p(H_2^2 - H_1^2)]$

[20d] $W_2 = N_2^{0.5}[W_1/N_1^{0.5} + 2.018p\displaystyle\int_{H_1}^{H_2} \Omega N^{-0.40422}H\,\mathrm{d}H]$

Table 3. Parameter estimates and fit statistics for the basal area sub-model ($b_2 = 1$). "Bias" is the mean of the residuals.

	b_1	b_3	c_1	c_2	RMSE	Bias	n	Plots
Shortest, raw	1.780	0.1081	0.01083	7141	3.100	0.3341	549	197
Shortest, smooth	2.907	0.05398	0.007863	9581	3.033	0.2814	487	168
From b.h., raw	2.018	0.09578	0.01023	8407	4.276	0.1786	549	197
From b.h., smooth	2.661	0.06518	0.008216	9432	4.315	0.2162	487	168

Note that this is age-independent, only the time interval $t_2 - t_1$ is needed.

Simulations from stand origin can be initialized at breast height with $H_1 = 1.3$, N_1 given, $B_1 = 0$, and

$$[21] \quad \Omega_1 = 1 - (1 - \max\{N_1/8407, 1\})^{2.6}$$

(c.f. equations [16] and [18]).

In thinning from below H is usually unchanged, with the density N_1 and basal area B_1 before thinning decreasing instantaneously to given values N_2 and B_2 after the thinning. The before-thinning Ω_1 changes to

$$[22] \quad \Omega_2 = 1 - \{1 - [1 - (1 - \Omega_1)^{1/2.6} B_2/B_1]\}^{2.6}.$$

If only one of the residual N_2 or B_2 is known, the other one can be estimated with relationships shown in the *Supplementary Material*.

4. Discussion and conclusions

The growth equations project H, N, B and Ω over time. Other quantities of interest can be estimated from regressions on the current value of these variables. Equations for total and merchantable volumes per hectare and for diameter distribution parameters are given in the *Supplementary Material*.

Unlike in other species, site indices in aspen reflect clonal differences in addition to differences in actual site quality (Penner *et al.*, 2001). The clonal spatial structure contributes to a high data variability and to uncertainty in growth forecasts. Another source of variability and uncertainty is the occurrence of stand breakup, and of occasionally catastrophic pest, drought, and other damage (Hogg *et al.*, 2008). Heavy mortality from these causes has been largely excluded from the model predictions, but the risk should be considered in forest planning.

The structure of the model allowed the components to be developed and evaluated sequentially: first height and site index as a self-contained sub-model, then mortality, assumed independent of basal area, and finally basal area parameters estimated conditionally on the previously fitted height and mortality models. Possible alternatives include simultaneous estimation in a multi-response setting (e.g. García, 1994), and multi-stage least-squares. The fact that we obtained practically the same predictions with four different estimation methods (weighted and unweighted with two types of intervals, also in García (2011)) suggests that, at least in this context, the choice of statistical procedures may not be too important.

The relative size of dying aspen trees, $k = 0.5$, was higher than the estimated 0.3 for interior spruce (García, 2011), and 0.4 for loblolly pine (García *et al.*, 2011). This would be expected from the differences in shade tolerance among the three species.

The general approach of García (2011) and García *et al.* (2011) proved satisfactory for modelling the growth of trembling aspen. However, the simplifying assumption $b_3 = k$ from the previous models was not acceptable, and therefore predictions require computing a numerical quadrature. This may be due in part to the higher k, and to the much wider range of densities in the aspen data.

Height projections were based on published site index models. This allowed a model to be built without ages, that are often missing or unreliable. Smoothing height increments to estimate the mortality and basal area parameters, which requires site quality estimates depending on age, was found not to be advantageous in this instance.

Imputation of tree observations missing due to minimum-dbh measuring thresholds improved data utilization and coverage of early stand development.

An easy-to-use and flexible spreadsheet-based implementation is available at `http://forestgrowth.unbc.ca/tag`. The differential equation formulation was also implemented in System Dynamics software, which produces results by numerical integration. Comparison of these values and the output from the spreadsheet transition functions provided confidence on the correctness of both versions.

As already mentioned, variability in the data is high (as noted by Flewelling *et al.*, 1996; Perala *et al.*, 1999), and individual stands can be expected to deviate considerably from the predictions. Nevertheless, the model should be a valuable addition to the tools currently available for planning the management of trembling aspen in Canada.

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