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ORIGINAL PAPER

Models relating stem growth to crown length dynamics: application to loblolly pine and Norway spruce

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Abstract We derive and analyze a model that relates the growth rate of cross-sectional area ('csa') at any height on the central stem of a tree to crown-length dynamics. The derivation is based, in part, on assumptions that (a) active csa on the central stem relates allometrically to the length of crown above the cross section, and (b) inactive csa is proportional to active csa within the crown. We also assume that the deactivation rate of csa beneath the crown is determined, in part, by the rate of crown rise. Integration of the growth-rate model under an additional assumption—that total crown length is constant after stand closure—provides a simple model of annual or periodic growth of total csa that can be fit to standard growth data. Three implications of the assumptions and integration are notable: (1) total csa within the crown scales allometrically with stem length above the cross section; (2) for a special case, total csa beneath the crown scales with stem length above the cross section; more generally, csa scales with a linear combination of the stem and crown lengths; and (3) the stem beneath the crown forms to approximate a frustum of a quadratic paraboloid. Basal area data from a loblolly pine (*Pinus taeda* L.) spacing trial show good agreement with (1) and (2), and with an empirical model developed from the special case of (2). Data from the plots of a Norway spruce (*Picea abies* (L.) Karst.) thinning trial, where crown length remained approximately constant, show good agreement with (2) and the empirical model. Prediction (3) is demonstrated by simulation.

Keywords Allometry · Growth model · Pipe model · Scaling · Stem form

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Introduction

Crown length is affected strongly by density (trees per unit land area) in stands of pines (*Pinus* sp.) and other species: the greater the density, the shorter the crown length (e.g., Beekhuis 1965; e.g., Valentine et al. 1994; e.g., Fish et al. 2006) and the smaller the girth of the average tree (e.g., Curtis and Reukema 1970; e.g., Valentine et al. 2000). Crown lengthen through height growth, and density also is known to influence the rate of height growth in all classes of trees, including dominant trees (e.g., Curtis and Reukema 1970; e.g., MacFarlane et al. 2000). The inference

from the combined work is that density constrains the size of a crown, and in so doing constrains the growth rate of the entire tree. Support for the inference is implicit in the successful forecasts of crown-based models, such as TASS (Mitchell 1975) or CROBAS (Mäkelä 1997), which estimate basal area growth from crown attributes, where the crown attributes encapsulate the effects of density.

A theoretical approach to explain the mechanism of how crown size affects basal area growth of the stem below the crown was proposed by Chiba et al. (1988) and Osawa et al. (1991) in the so-called profile theory of tree growth. The crown profile theory is a further development of the pipe model theory (Shinozaki et al. 1964), according to which the active stem wood cross-sectional area at any height along the stem is proportional to the foliage mass above. The pipe model theory also postulates that as the crown rises, the active pipes are deactivated and accumulate as heartwood. Using the simplifying assumptions that crown shape and size, as well as height growth rate were constant over time, Osawa et al. (1991) were able to derive reasonable approximations of stem profiles and branchiness for several tree species. Mäkelä (2002) generalized the crown profile theory by allowing for dynamic crown size and height growth in a model based on the carbon metabolism and optimal crown allometry (Mäkelä and Sievänen 1992). These assumptions resulted in successful predictions of basal area growth rates and stem shapes in Scots pine (*P. sylvestris* L.) growing in different stand densities.

The 'bridging model' of tree growth (Valentine and Mäkelä 2005) is formulated as a process-based model that can be fitted and applied in an empirical mode. The process assumptions are similar to those used by Mäkelä (2002), but with the explicit objective of simplicity in the formulation, which affords consolidation, resulting in an empirical model with relatively few parameters. Cross-sectional area growth at any height on the bole beneath the crown of a model tree is explicitly formulated as a function of crown length dynamics. Annual changes in the tip and base heights of a crown depend on the carbon metabolism and spatial constraints, and the growth of bole cross-sectional area is completely determined by the crown length dynamics, as manifested by changes in the tip and base heights. Tree density (or tree spacing) affects cross-sectional area growth indirectly through its effects on both height growth and crown length. A year-to-year picture of the development of the stem profile is achieved by keeping track of cross-sectional area at different heights on the stem beneath the crown.

Due to its simplicity, the bridging model expresses the underlying assumptions of the profile theory combined with carbon metabolism and optimal crown allometry in a form that conveniently lends itself to testing the implications of the assumptions against standard forestry data, e.g., from spacing or stocking trials. An objective of this paper is to carry out such a test, using data from a loblolly pine (*P. taeda* L.) spacing trial and a Norway spruce (*Picea abies* (L.) Karst.) thinning trial. However, our first objective is to modify the bridging model to allow for the deactivation of pipes (or heartwood formation) within the crown, which has been observed empirically (e.g., Longetaud et al. 2006).

The modification primarily concerns model parameterization and includes the original bridging model as a special case. The resultant modified model predicts cross-sectional growth rate at any height on the stem above the buttswell. Under specific assumptions, integration of the growth-rate model provides models of annual or periodic growth in the form of difference equations, which can be readily fit to standard growth data. We provide three such models: the first applies within the crown of a model tree, under the assumption that active cross-sectional area is either proportional or equal to total cross-sectional area. The second and third models—the third a special case of the second—apply beneath the crown, under the additional restrictive assumption of constant crown length after stand closure. A fourth model, which is not a derived result, is formulated to afford statistical testing of the third model, which has no parameters.

We begin with the derivation of the growth models, followed by our fitting procedures and the results. In the final section, we discuss, among other things, the implications of the model for predicting the development of stem profiles. The results of some stem-profile simulations are provided.

Materials and methods

The model

The model of cross-sectional area growth derives from an allometric model (Valentine and Mäkelä 2005) that, in turn, derives from the pipe model (Shinozaki et al. 1964) and a model of optimal crown development (Mäkelä and Sievänen 1992). The allometric model relates A_h, the cross-sectional area of active pipes at height h on the central stem of a tree, to the length of crown above height h. Let z be the scaling exponent, then

$$A_h = \begin{cases} \beta L_h^z, & 0 < L_h \leq L_c \\ \beta L_c^z, & L_h > L_c \end{cases} \quad (1)$$

where $L_c = H - H_c$ is crown length, H is height of the crown tip, H_c is height of the crown base, $L_h = H - h$ is the distance from the crown tip down to height h on the central stem, and β is the normalization constant. We assume that the model for $L_h \leq L_c$ applies until the onset of crown rise, even at the ground line.

The time derivative of (1) is

$$\frac{\mathrm{d}A_h}{\mathrm{d}t} = \begin{cases} z\left(\frac{A_h}{L_h}\right)\frac{\mathrm{d}L_h}{\mathrm{d}t}, & L_h \le L_c \\ z\left(\frac{A_c}{L_c}\right)\left(\frac{\mathrm{d}L_h}{\mathrm{d}t} - \frac{\mathrm{d}H_c}{\mathrm{d}t}\right), & L_h < L_c \end{cases} \quad (2)$$

since $\mathrm{d}L_h/\mathrm{d}t \equiv \mathrm{d}H/\mathrm{d}t$ and $\mathrm{d}L_c/\mathrm{d}t \equiv \mathrm{d}L_h/\mathrm{d}t - \mathrm{d}H_c/\mathrm{d}t$.

Let A_h^+ be the total cross-sectional area at h and let A_h^- be the cross-sectional area of deactivated pipes, so $A_h \equiv A_h^+ - A_h^-$. Valentine and Mäkelä (2005) associated the deactivation of pipes with crown rise—pipes that extend into branches at the base of the crown deactivate as the branches die. For the present model, we also allow for deactivated pipes within a live crown such that $A_h^- = \eta A_h$. We assume a constant coefficient of proportionality ($0 < \eta < 1$), with a limiting case ($\eta = 0$) indicating no deactivated pipes within the crown.

Substituting $A_h^+ - A_h^-$ on the left-hand side of (2) and adding zero, i.e., $\eta(\cdot) - \eta(\cdot)$, to the right hand side,

$$\frac{\mathrm{d}A_h^+}{\mathrm{d}t} - \frac{\mathrm{d}A_h^-}{\mathrm{d}t} = \begin{cases} z\left(\frac{A_h}{L_h}\right)\left(\frac{\mathrm{d}L_h}{\mathrm{d}t} + \eta\frac{\mathrm{d}L_h}{\mathrm{d}t} - \eta\frac{\mathrm{d}L_h}{\mathrm{d}t}\right), & L_h \le L_c \\ z\left(\frac{A_c}{L_c}\right)\left(\frac{\mathrm{d}L_h}{\mathrm{d}t} - \frac{\mathrm{d}H_c}{\mathrm{d}t} + \eta\frac{\mathrm{d}L_c}{\mathrm{d}t} - \eta\frac{\mathrm{d}L_c}{\mathrm{d}t}\right), & L_h > L_c \end{cases} \quad (3)$$

At first glance, the zeros added to the two cases of (3) appear to differ. However, $\mathrm{d}L_h/\mathrm{d}t$ is the rate of change of crown length above height h when h occurs within the crown, and $\mathrm{d}L_c/\mathrm{d}t$ is the rate of change of crown length above height h, when h occurs beneath the crown. The value of η is the same for both cases.

Active and deactivated cross-sectional area, respectively, often are interpreted as sapwood and heartwood. Regardless, from a pipe model perspective, $\mathrm{d}A_h^+/\mathrm{d}t$ is both the rate of gain of new active cross-sectional area and the growth rate of total cross-sectional area at h; $\mathrm{d}A_h^-/\mathrm{d}t$ is the rate of loss of active cross-sectional area, which is equivalent to the rate of gain of deactivated cross-sectional area at h. The difference, $\mathrm{d}A_h/\mathrm{d}t \equiv \mathrm{d}A_h^+/\mathrm{d}t - \mathrm{d}A_h^-/\mathrm{d}t$, is the growth rate (i.e., the rate of gain less the rate of loss) of active cross-sectional area.

Following the strategy of Valentine and Mäkelä (2005), we decompose (3) into separate equations for $\mathrm{d}A_h^-/\mathrm{d}t$ and $\mathrm{d}A_h^+/\mathrm{d}t$. We assume that all the active pipes, which run from the central stem into branches at the base of a crown, deactivate when the branches die. Consequently, the rate of deactivation beneath the crown is determined, in part, by the rate of crown rise ($\mathrm{d}H_c/\mathrm{d}t$). In addition, the rate of deactivation beneath/within the crown is determined partly/wholly by our assumption of fixed proportionality between active and deactivated pipes that run up the central stem and into branches within the live crown. So, in effect, we associate $-\mathrm{d}A_h^-/\mathrm{d}t$ with the negative terms on the right-hand side of (3). The model for $\mathrm{d}A_h^+/\mathrm{d}t$ follows algebraically, whence

$$\frac{\mathrm{d}A_h^-}{\mathrm{d}t} = \begin{cases} z\eta\left(\frac{A_h}{L_h}\right)\frac{\mathrm{d}L_h}{\mathrm{d}t}, & L_h \le L_c \\ z\left(\frac{A_c}{L_c}\right)\left(\frac{\mathrm{d}H_c}{\mathrm{d}t} + \eta\frac{\mathrm{d}L_c}{\mathrm{d}t}\right), & L_h > L_c \end{cases} \quad (4)$$

and

$$\frac{\mathrm{d}A_h^+}{\mathrm{d}t} = \begin{cases} z\left(\frac{A_h}{L_h}\right)\left((1+\eta)\frac{\mathrm{d}L_h}{\mathrm{d}t}\right), & L_h \le L_c \\ z\left(\frac{A_c}{L_c}\right)\left(\frac{\mathrm{d}L_h}{\mathrm{d}t} + \eta\frac{\mathrm{d}L_c}{\mathrm{d}t}\right), & L_h > L_c \end{cases} \quad (5)$$

Note that subtraction of (4) from (5) yields (2), so this model accords with the pipe model and the optimal crown model. Moreover, the cross-sectional growth rate is uniform at all heights on the stem beneath the crown base, so this model also accords with 'Pressler's law' (e.g., Assmann 1970). If $\eta = 0$, then (5) reduces to the model proposed by Valentine and Mäkelä (2005). However, if $\eta > 0$, then, as we show later, (5) provides not only for heartwood within a crown, but also for the development of a paraboloidic bole with a juvenile core.

From (2) and (5), $A_h^+ = (1+\eta)A_h$ for $L_h \le L_c$. Substituting this result into (5), we obtain our general model of cross-sectional area growth:

$$\frac{\mathrm{d}A_h^+}{\mathrm{d}t} = \begin{cases} z\left(\frac{A_h^+}{L_h}\right)\frac{\mathrm{d}L_h}{\mathrm{d}t}, & L_h \le L_c \\ \frac{z}{1+\eta}\left(\frac{A_c^+}{L_c}\right)\left(\frac{\mathrm{d}L_h}{\mathrm{d}t} + \eta\frac{\mathrm{d}L_c}{\mathrm{d}t}\right), & L_h > L_c \end{cases} \quad (6)$$

Since A_c^+ occurs on the right hand side of the second case, we require

$$\frac{\mathrm{d}A_c^+}{\mathrm{d}t} = z\left(\frac{A_c^+}{L_c}\right)\frac{\mathrm{d}L_c}{\mathrm{d}t} \quad (7)$$

for simultaneous integration. Note that (7) is equivalent to (6) for $L_h = L_c$.

Within the crown

Let us examine (6) for the case where $L_h \le L_c$, i.e., h occurs within the crown. If $\eta > 0$, then the total cross-sectional area at height h on the main stem is modeled by $A_h^+ = (1+\eta)\beta L_h^z$, and active cross-sectional area is modeled by $A = \beta L_h^z$. If $\eta = 0$, deactivated cross-sectional area does not occur within the crown, so $A_h^+ = A_h = \beta L_h^z$. Regardless of whether $\eta = 0$ or $\eta > 0$, division of the model for time $t + k$ by that for time t yields the growth model

$$A_h^+(t+k) = A_h^+(t)\left(\frac{L_h(t+k)}{L_h(t)}\right)^z, \quad 0 < L_h \le L_c \quad (8)$$

Beneath the crown

Now let us derive a growth model from (6) and (7) for the case $L_h > L_c$, i.e, h occurs beneath the crown. Crown length may remain approximately constant after the onset of crown rise ($dL_c/dt \approx 0$), in which case (A_c^+/L_c) is constant for the model tree, so

$$\frac{dA_h^+}{dL_h} = \frac{z}{1+\eta}\left(\frac{A_c^+}{L_c}\right), \quad L_h > L_c \tag{9}$$

Integration, i.e.,

$$\int_{A_c^+}^{A_h^+} dA_h^+ = \frac{z}{1+\eta}\left(\frac{A_c^+}{L_c}\right)\int_{L_c}^{L_h} dL_h \tag{10}$$

provides

$$\frac{A_h^+ - A_c^+}{L_h - L_c} = \lambda\left(\frac{A_c^+}{L_c}\right) \tag{11}$$

or, identically,

$$\frac{A_h^+}{L_h + vL_c} = \frac{A_c^+}{L_c + vL_c} \tag{12}$$

where $\lambda = z/(1+\eta)$ and $v = (1-\lambda)/\lambda$. Because the right hand side of (12) is constant, it follows that $A_h^+/(L_h + vL_c)$ is also constant. Consequently, under our assumptions, A_h^+ scales with a linear combination of the stem length, L_h, and the constant crown length, L_c, i.e., $A_h^+ \propto (L_h + vL_c)$.

Division of (12) at time $t+k$ by the same relation at time t yields the growth model

$$A_h^+(t+k) = A_h^+(t)\left(\frac{L_h(t+k) + vL_c}{L_h(t) + vL_c}\right) \tag{13}$$

In reality, crown length, $H - H_c$, is expected to be approximately, rather than truly, constant from year to year owing to the nodal nature of both height growth and crown rise. So, for fitting purposes, we suggest,

$$A_h^+(t+k) = A_h^+(t)\left(\frac{L_h(t+k) + vL_c(t+k)}{L_h(t) + vL_c(t)}\right) \tag{14}$$

If, perchance, $\eta = z - 1$, then $\lambda = 1$ and $v = 0$, and so (13) and (14) simplify to

$$A_h^+(t+k) = A_h^+(t)\left(\frac{L_h(t+k)}{L_h(t)}\right) \tag{15}$$

Equations (11) and (12) are renderings of a de facto stem profile model which indicates that cross-sectional area (or the radius-square) of the model bole at h increases linearly with the stem length, L_h. Thus, given constant crown length after the onset of crown rise, (6), (13), and (15) will cause the section of the model bole beneath the crown and above the buttswell to form as a frustum of a quadratic paraboloid. In effect, (11) and (12) are static versions, and (13) and (15) are dynamic versions, of the taper-line model of Gray (1956).

The need for crown length vanishes if $v \approx 0$, reducing (13) and (14) to (15). The latter model may be a reasonable choice if crown lengths are unavailable for fitting (13) or (14). Alternatively, we could fit a modified version of (15) that incorporates a parameter (α), e.g.,

$$A_h^+(t+k) = (1+\alpha)^k A_h^+(t)\left(\frac{L_h(t+k)}{L_h(t)}\right) \tag{16}$$

If an estimate of α is significantly different from 0, then (16) differs from (15).

Of special interest is basal area, A_b^+, which, by convention, is cross-sectional area at breast height ($h = b$). Hence, $L_b = H - b$ is the distance from the crown tip to breast height, and L_c/L_b is crown ratio above breast height. In the remainder of the paper, we shall refer to growth models of basal area by their parameters: hence (8) is model z, (14) is model v (15) is model 0 since it has no parameters, and (16) is model α.

Loblolly pine: data and analysis

Loblolly pine data were gathered from spacing trials maintained by the Forest Modeling Research Cooperative at Virginia Tech. Initiated in 1983, the spacing trials comprise three replications of 16 different spacing patterns, resulting in 9 distinct densities (ranging from 747 to 6,727 stems ha^{-1}) at each of four locations—Buckingham, Halifax, and King and Queen Co., Virginia, and Halifax Co., NC. The experimental design follows from Lin and Morse (1975). Details of the design, as applied to the Virginia Tech spacing trials, are provided by Amateis et al. (1988). Other analyses of these spacing trial data were reported by Zhang et al. (1996), Sterba and Amateis (1998), and MacFarlane et al. (2000). In addition, a process-based, stand-level, growth model was calibrated, in part, from these data (Valentine et al. 1997).

The requisite data for our purpose were gathered from ages 2 to 25 years. Observation sets comprising ground-line diameter, height, and height of the crown base were measured from age 2 to 5; dbh was measured from age 5 to 25 (Fig. 1). Some plots were dropped from the study following an ice storm; in others, data gathering was stopped following the storm, then resumed a few years later. Height to the base of the crown was measured every other year after age 10, so we interpolated values of crown length between measurements.

We limited the analysis to the 83,548 observation sets for individual trees in which $A_b^+(t+1) > A_b^+(t)$, $L_b(t+1) > L_b(t)$, and $H_c(t+1) \geq H_c(t) > 1.5$ m. The trees in four plots within each replicate within each location of the trial were

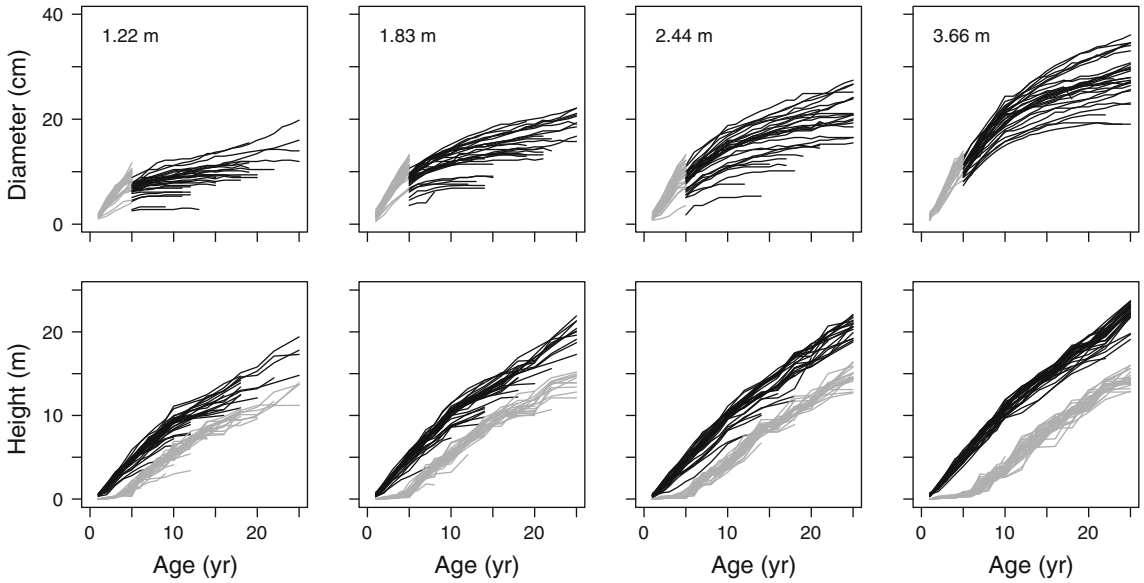

Fig. 1 Loblolly pine data by initial spacing, from one replicate of the spacing trial. *Diameter graphs*: ground line (*gray*), breast height (*black*). *Height graphs* crown base (*gray*), tip height (*black*)

planted with square spacing: 1.22, 1.83, 2.44, or 3.66 m. Each of the other plots had rectangular spacing, employing two of these four spacings, e.g., 1.22 × 1.83, 1.22 × 2.44, and so forth.

We performed systematic sampling of the observation sets in square-spaced plots to extract observation sets for model fitting. We also performed a 1-in-20 systematic sampling of observation sets in all plots, and used these observation sets for model evaluation. The systematic samplings precluded the occurrence of more than two observation sets per tree in the fitting and evaluation datasets.

We fit the models by nonlinear regression in *R* (*R* Development Core Team 2010). Model z was fit with a 1-year time step; models α and ν were fit with three different time steps, i.e., $k = 1$, 2, and 4 years.

Norway spruce: data and analysis

Norway spruce data were gathered from an even-aged thinning experiment in a pure Norway spruce stand in southern Finland (61°12′N, 26°00′E). The experiment was established in 1962 by the Finnish Forest Research Institute in a normal commercial forest on mineral soil. The stand had been planted in 1926 using seedlings grown 4 years in a nursery. The site was classified as belonging to the *Oxalis–Myrtillus* forest site type (Cajander 1949), which corresponds to highly fertile sites (site index = 34.7 m at 100 years) (Vuokila and Väliaho 1980).

After establishment, the experiment had been measured eight times and thinned from below three times. The experiment had eight plots (0.1 ha, surrounded by a 5-m buffer zone) with four different thinning intensities: none, light, moderate, or heavy, the most intensively thinned.

Stem diameter at breast height and possible damage (fallen, broken, decaying, needle loss, etc.), as well as its cause (wind, snow, competition, insect or fungus species) and severity (temporary, causing permanent defects, lethal), were recorded for each tree on the plot. The trees were remeasured on intervals of $k = 2$, 4, 5, or 7 years.

At the time of establishment of the experiment, sample trees had been selected from every plot. The selection of sample trees was with probability proportional to diameter, but the distribution of sample tree locations across the plot had a random pattern. Tip height, height to crown base, and stem diameter at 6 m height were measured on each sample tree. The crown base was defined as the lowest whorl with at least one living branch that was separated from the other living whorls above it by no more than one dead whorl. A sample of the data is depicted in Fig. 2. Growth and yield results and other analyses based on this experiment were reported by Vuokila (1975) and Mäkinen and Isomäki (2004a, b).

We fit models ν and α by nonlinear regression with 1,279 sets of tree observations from 8 plots, after subjecting the raw data to the same editing procedures as loblolly pine. We also formulated models with indicator variables, so the parameters could take a different value for each of the four thinning intensities. We could not fit model z, as all crowns had risen above breast height before the first measurement.

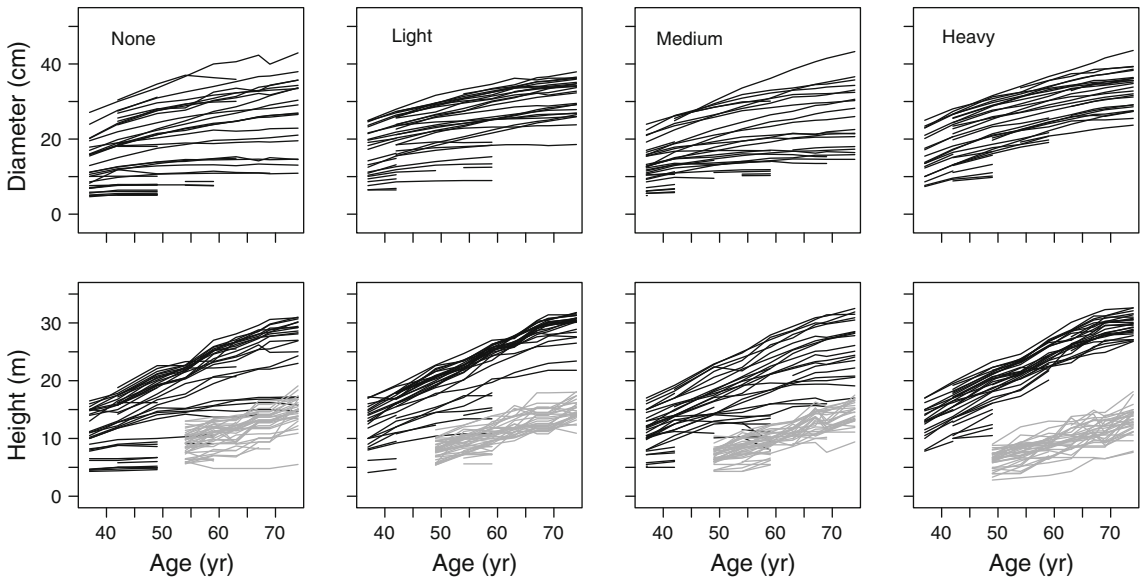

Fig. 2 Norway spruce data by thinning treatment. height graphs: crown base (*gray*), tip height (*black*)

Results

Model *v* is the best performing model of basal area growth for both loblolly pine and Norway spruce, when breast height occurs beneath the crown. Model α is next best, though our estimate of α is not significantly different from zero for a 2-year time step for loblolly pine. Model 0 is a competitive model, with only slightly larger residual standard errors (Tables 1, 2) and a slight under-estimation bias, as compared to models α and *v* (Figs. 3, 4). This bias notwithstanding, application of model 0 to project loblolly basal area, tree by tree, from age 5 to 25 gives realistic results (Fig. 5). Results from the fit of model z are provided in Table 1.

The analysis of variance indicated that crown lengths in the lightly or heavily thinned Norway spruce plots increased significantly between measurement time steps, which conflicts with the underlying assumptions of both models *v* and 0. Therefore, we provide estimates in Table 2 without regard to thinning level, and a second set of estimates for the non and moderately thinned plots, which kept fairly constant crown lengths in concordance with the assumptions. Projections with the model for all thinning levels are reasonable, though under-estimation, as expected, is evident in tree-by-tree projections within the heavily thinned plots (see Fig. 6).

In general, the residual standard errors increase with the time steps of the different models, i.e., the value of *k*. The error for loblolly pine with a 4-year time step is similar to the error estimated for Norway spruce, for which the measurement interval varied from 2 to 7 years (see Tables 1, 2).

Discussion

The bridging model (Valentine and Mäkelä 2005) was formulated from theory with a minimalist philosophy: (a)

Table 1 Estimates for the loblolly pine models z, α, *v*, and 0 by timestep (*k*) in years

Parameter	*k*	Estimate	Standard error	*t*	Pr($>\|t\|$)	Rse
z	1	1.7808	0.0098	181.9	<0.0001	1.03
α	1	0.0061	0.0011	5.64	<0.0001	11.0
	2	0.0011	0.0009	1.11	0.268	19.2
	4	0.0020	0.0007	3.06	0.0022	27.9
v	1	−0.1785	0.0186	−9.61	<0.0001	10.9
	2	−0.1479	0.0181	−8.16	<0.0001	18.7
	4	−0.1362	0.0156	−8.70	<0.0001	27.2
0	1					11.1
	2					19.1
	4					27.9

Rse (cm^2) is the estimate of residual standard error

Table 2 Estimates for the Norway spruce models α, v, and 0: (a) without regard to thinning level; and (b) eliminating light and heavy thinning levels

Parameter	Thinning	Estimate	Standard error	t	Pr($>\|t\|$)	Rse
α	a	0.0036	0.00028	13.27	<0.0001	31.3
	b	0.0029	0.00033	8.64	<0.0001	28.8
v	a	−0.1957	0.01605	12.19	<0.0001	31.9
	b	−0.2104	0.01862	11.3	<0.0001	28.5
0						32.1

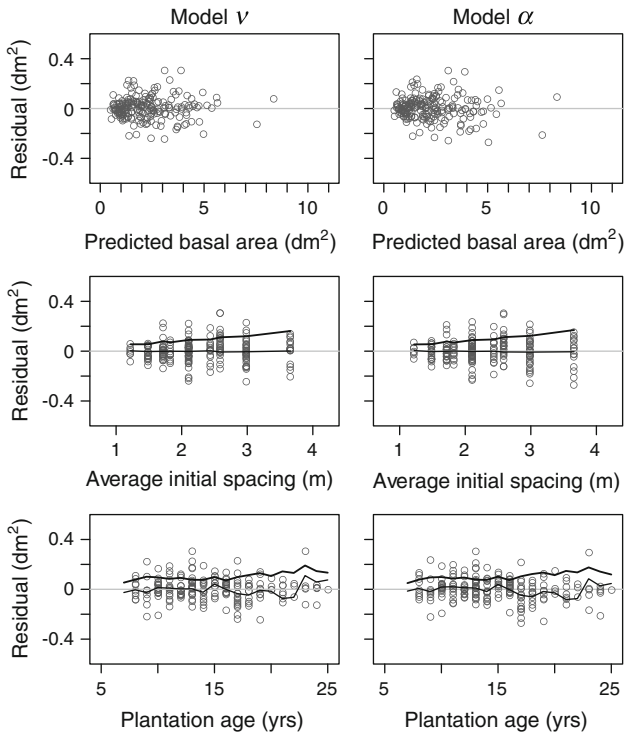

Fig. 3 A systematic subset of residuals of basal area for loblolly pine versus predicted basal area, intial spacing, and plantation age. *Trend lines* for the residual standard errors are *thick*, the mean-residual trend lines are *thin*

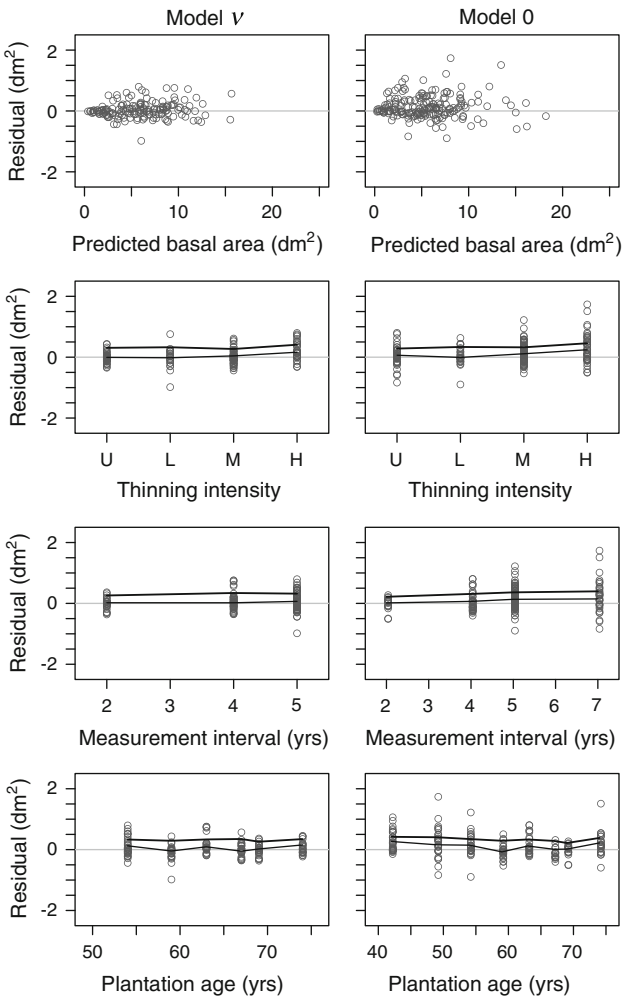

Fig. 4 A systematic subset of residuals of basal area for Norway spruce versus predicted basal area; the growth interval, k, between remeasurements; thinning treatment (U unthinned, Llight, M moderate, H heavy), and plantation age. *Trend lines* for the residual standard errors are *thick*, the mean-residual trend lines are *thin*

parameterizations of carbon gain and allocation based on physiology, an optimal crown model, and pipe model theory determine height growth, (b) height growth and local tree spacing determine changes in crown length, and (c) annual changes in crown length and adherence to the pipe model determine cross-sectional area growth at any height beneath the crown base. An empirical model of height growth may substitute for the process-based height growth model in (a).

In this paper, we elaborated (c). As was noted, the model of cross-sectional area growth derives from an allometric relation between sapwood cross-sectional area beneath the crown and crown length, i.e., $A_c = \beta\ L_c^z$. The resultant growth model, (6), allows for heartwood development within the crown, based on the assumption that heartwood cross-sectional area is proportional to sapwood. This is similar to an assumption used by Mäkelä and Valentine (2006) in a theoretical study of the fractal dimension of a crown. A conclusion from that study was that any relation between basal area and crown length or height depends on the history of the crown dynamics, which integrates the

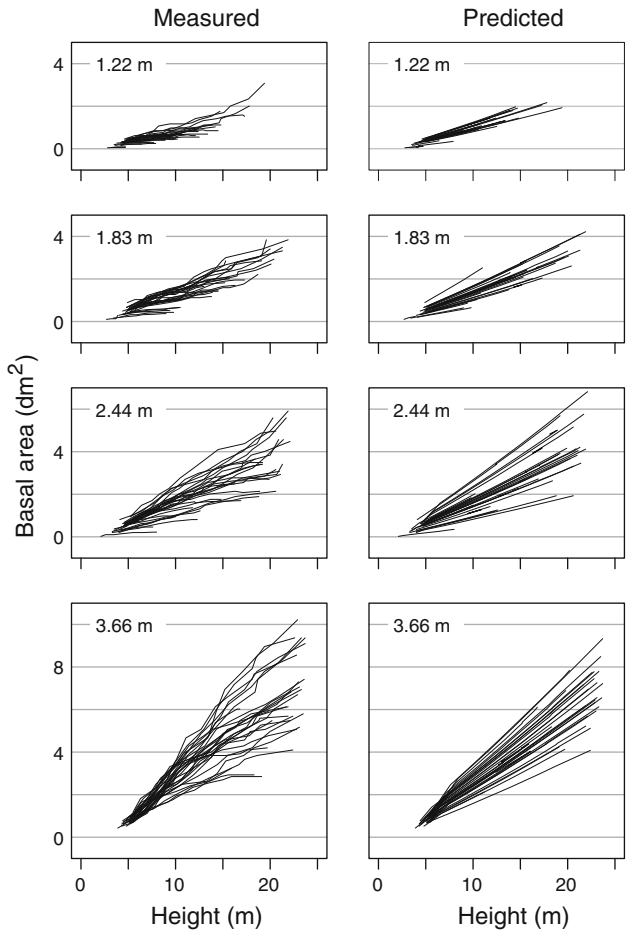

Fig. 5 Measured and predicted basal areas (5–25 years from planting) versus actual heights of loblolly pine trees at four spacings. Predictions for each tree were calculated with model 0, which was initialized with true basal area at 5 years from planting. Kinks in some predicted trajectories occur where crown bases rise above breast height

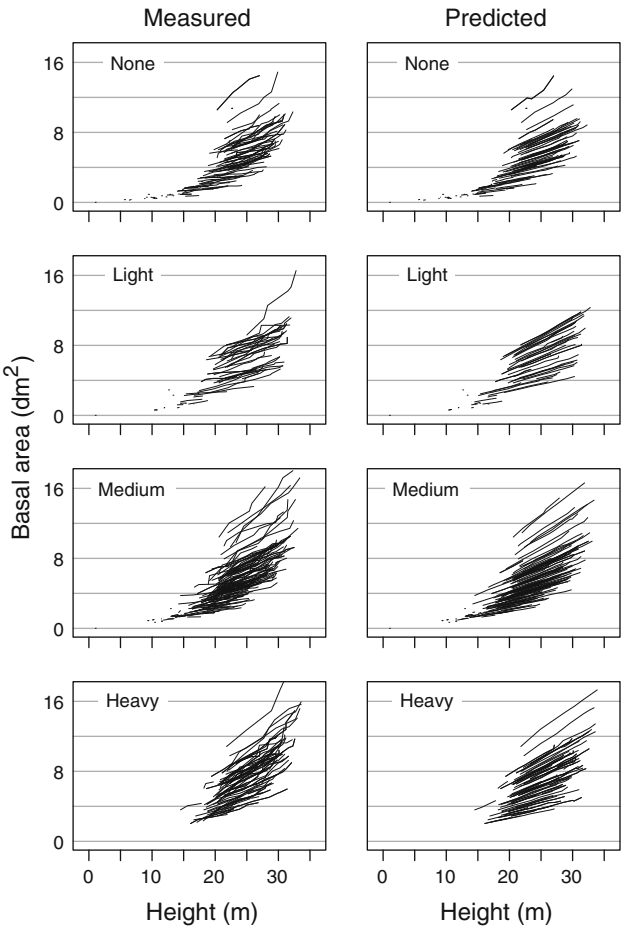

Fig. 6 Measured and predicted basal areas (49–74 years from planting) versus actual heights of Norway spruce trees by thinning treatment (none, light, medium, or heavy). Predictions for each tree were calculated with model *v*, which was initialized with true basal area the first year that crown length was measured

effects of spacing over time. An identical conclusion can be drawn from this study, although we have now isolated a situation—a closed stand with approximately constant crown length—where the relation between basal area and height of a tree tends to be isometric. In our formulation of this model, deactivated sapwood (or heartwood) cross-sectional is ηA_c at the base of the crown, so $\eta/(1+\eta)$ is the ratio of deactivated to total cross-sectional area.

Under the constant crown-length restriction, the derived model, (6), simplifies to (14), which we have called model *v*. The value of the parameter, *v*, may be positive, negative, or 0. Model 0 results if *v* equals 0. Model α is a tweak of model 0 rather than a derived result. With each of the three alternative models, each tree assumes its own trajectory, which is determined by the initial values of A_b^+ and L_b, as shown in Figs. 5 and 6.

Models 0 and α do not require knowledge of crown length. A value of α that differs just slightly from 0 will cause some curvature in the trajectory of cross-sectional area versus height. A positive value causes the ratio $A_h^+(t+k)\ /\ A_h^+(t)$ to increase faster than the ratio $L_h(t+k)/L_h(t)$, so the slope, $\mathrm{d}A_h^+/\mathrm{d}L_h$, increases gradually with L_h. Conversely, a negative value of α causes a decreasing slope. We see slight changes in slope in both directions in Figs. 5 and 6. Hence, a mixed-model fit is suggested if model α is to be used for application in a tree-based model of stand growth. Alternatively, a Bayesian fit provides the posterior distribution of parameter values.

Mäkelä (2002) provided a dynamic model of the development of a stem and its taper from pipe model theory in a carbon balance framework. The present model is less detailed than Mäkelä's model, but, nonetheless, it also can be set-up as a dynamic model of stem development. Because the present model provides cross-sectional area growth at any height, we can model the development of the

stem profile as the tree grows in height. As was noted, $A_h^+ = \beta(1 + \eta)\, L_h^z$ for $L_h \le L_c$. Substituting into (6) yields

$$\frac{dA_{h_i}^+}{dt} = \begin{cases} \beta z L_{h_i}^{z-1}\left((1+\eta)\dfrac{dL_{h_i}}{dt}\right), & L_{h_i} \le L_c \\ \beta z L_c^{z-1}\left(\dfrac{dL_{h_i}}{dt} + \eta\dfrac{dL_c}{dt}\right), & L_{h_i} > L_c \end{cases} \quad (17)$$

With this substitution, $A_{h_i}^+$ can take an initial value of zero, so we can begin to estimate $A_{h_i}^+$ when the tree tip reaches height h_i, where, for example, i may index the ith annual height node. We implemented this model in *R*, along with the height growth and crown-rise models suggested by Valentine and Mäkelä (2005). The set of differential equations was solved with package deSolve (see Soetaert et al. 2010). The solution comprises time courses of basal area, height, and crown height, as well as time-courses of cross-sectional areas at annual nodes between breast height and the tip height. Partial verification of a profile diagram is achieved with good agreement with actual time courses of basal area, height, and crown height. However, a thorough test of paraboloidic form is obviated by a lack of cross-sectional measurements at heights above breast height.

Stem profiles, constructed from the predicted time courses, are depicted in Fig. 7 for $\eta = 0.4$, 0.8, or 1.2, with $z = 1.8$ and $\beta = 3.11$ ($cm^2 m^{-z}$). Note that the radius and cross-sectional area of the juvenile core wood—wood formed while h_i is within the crown of a model tree—increases with the value of η. We speculate that the value of η may relate to the specific wood volume (i.e., wet volume per unit dry mass) of the juvenile core.

The parameter estimates from this study, whether 0 or otherwise, could be used in a working model of tree growth, although it might be better to pursue a simultaneous fit of the basal area growth model and the growth models of the tip and base height of the crown. Options and considerations for empirical and process-based modeling of the tip and base heights of crowns of individual trees were discussed by Valentine and Mäkelä (2005) in connection with the formulation of a basal area growth model.

In summary, the principal contribution of this paper is the derivation of a simple growth model that relates cross-sectional growth to crown-length dynamics, allowing for deactivated wood in the central stem of the crown. The growth model predicts, in closed stands, that the boles will form to approximate quadratic paraboloids. This finding is an emergent property of the model.

We caution, however, that the loblolly pine spacing trials and the Norway spruce thinning trials were not geographically extensive, so our results for these species may not extrapolate to other areas, environments, or situations. The model has not been tested for broadleaved species. Moreover, the results may not extrapolate to stands approaching senescence. The model can, no doubt, be improved. Nonetheless, this study provides evidence that rather minimal data—just annual or periodic changes in tip height and base height—can be used to estimate cross-sectional growth and the development of stem taper in boreal and temperate conifers over a range of spacings.

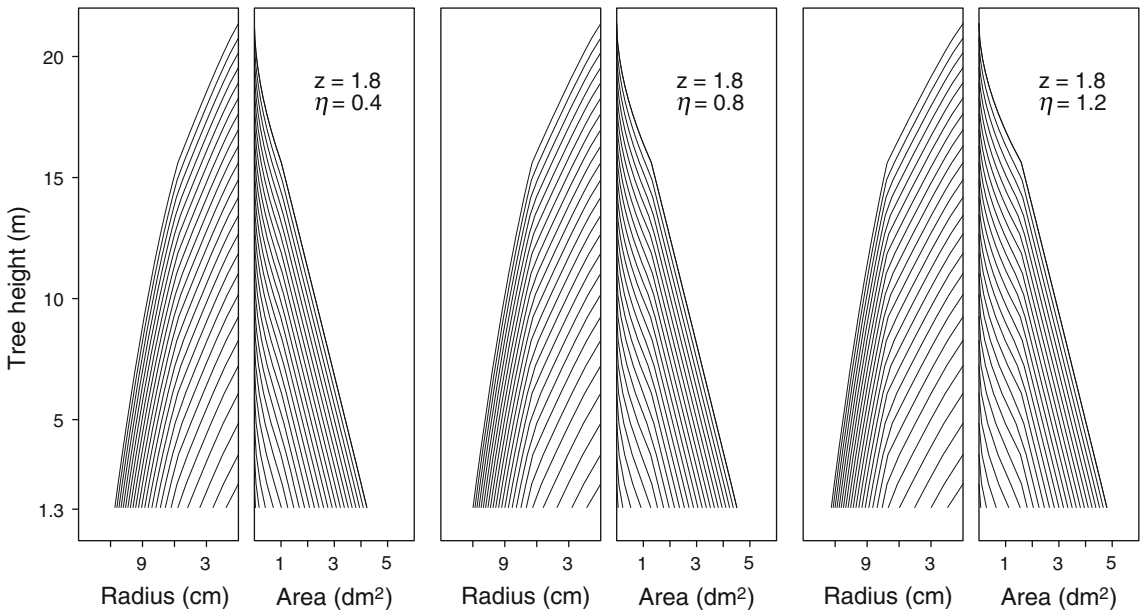

Fig. 7 Modeled radial and cross-sectional area profiles from tree tip to breast height, by year, with $z = 1.8$ and $\eta < z - 1$ (*left*), $\eta = z - 1$ (center), and $\eta > z - 1$ (*right*). Profiles were calculated with (17) with 2.44-m spacing

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