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Crown-rise and crown-length dynamics: application to loblolly pine

Harry T. Valentine[1]*, Ralph L. Amateis[2], Jeffrey H. Gove[1] and Annikki Mäkelä[3]

[1]*U.S. Forest Service, 271 Mast Road, Durham, NH 03824-6400, USA*
[2]*College of Natural Resources and Environment, VPI & SU, 304-A Cheatham Hall (0324), Blacksburg, VA 24061, USA*
[3]*Department of Forest Sciences, PO Box 27, 00014 University of Helsinki, Finland*

*Corresponding author. Tel: +1 603 868 7671; E-mail: hvalentine@fs.fed.us

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The original crown-rise model estimates the average height of a crown-base in an even-aged mono-species stand of trees. We have elaborated this model to reduce bias and prediction error, and to also provide crown-base estimates for individual trees. Results for the latter agree with a theory of branch death based on resource availability and allocation. We use the improved model to estimate the growth and stem-profile development of a mean-tree in an even-aged stand of loblolly pine. Predictions show good agreement with data from a loblolly pine spacing trial.

Introduction

The crown-length dynamics of trees comprise temporal changes in tip and base heights of their live crowns. Tip heights either increase by primary growth, utilizing products of photosynthesis, or decrease owing to dieback or injury. Base heights of crowns rise as the lowest branches die, most likely due to factors associated with crowding by adjacent crowns, insufficient photosynthesis to meet maintenance respiration costs, and evolved within-crown carbon-allocation patterns that seem to favour the success of higher branches, especially within the crowns of more vigorous trees (Sprugel, 2002).

Crown-length dynamics play out in a fairly predictable course in plantations of loblolly pine (*Pinus taeda* L.), especially where the distance (or spacing) among trees is uniform and weed competition is minimal. After establishment, crowns lengthen by height growth, with little or no rise in the base heights of the crowns until closure; then the average crown length becomes approximately constant, with crown rise keeping pace with height growth, until differentiation and self-thinning ensue. The behaviour is predicted by the so-called ‘crown-rise model’, which estimates the base height of a tree crown from average tree height and spacing (Valentine *et al.*, 1994).

The original crown-rise model estimates the yearly or periodic change in the average base height of tree crowns (‘crown height’) in an even-aged stand. A tree-level adaptation of the original crown-rise model requires location coordinates for every tree (Valentine *et al.*, 2000). Pruves *et al.* (2007) provided an alternative model of crown metrics.

In this note, we tweak the original stand-level crown-rise model to improve its performance. We also provide for the estimation of individual crown heights without need for tree locations. Finally, we demonstrate how the crown-rise model can be embedded within a tree dynamics model to predict either a time-course of dbh or the development of a diameter profile of an entire central stem or both.

Original crown-rise model

Let H (m) be the average tree height (‘tip height’) in an even-aged stand and H_c (m) be crown height – the height to the base of a crown. The dynamics of the crown-rise model are determined by three assumptions: (i) the average crown length in a closed stand is proportional to the average spacing among trees (X, m), i.e. $H - H_c = \beta X$, so $H_c = H - \beta X$, where β is a parameter; (ii) between stand establishment and closure, the average crown length equals average tree height, i.e. $H - H_c = H$, so $H_c = 0$; (iii) after a thinning or pruning in year $t-1$, crown height is constant until the stand re-closes, so $H_c(t) = H_c(t-1)$. Combining the three assumptions into a single crown-rise model,

$$H_c(t) = \max[0, H_c(t-1), H(t) - \beta X(t)] + \epsilon \tag{1}$$

where ϵ is residual error. The average spacing is defined by the stand density, i.e. the number of trees per unit land area. Let N (m^{-2}) denote the stand density, then $X \equiv \sqrt{1/N}$.

The second assumption of the model – no crown rise before stand closure – often is not accurate owing to weed competition and self-shading. A simple alternative, in this case, is to assume that crown height is proportional to average tree height, i.e. $H_c = \nu H$ $(0 \le \nu < 1)$, whence

$$H_c(t) = \max[\nu H(t), H_c(t-1), H(t) - \beta X(t)] + \epsilon \tag{2}$$

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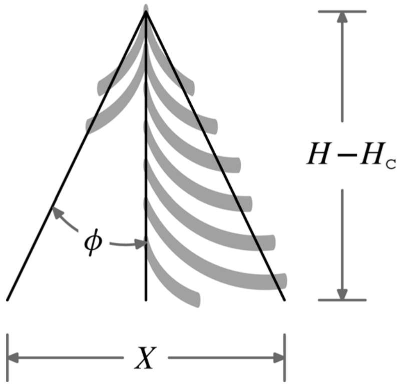

Figure 1 The angle ϕ defines a conceptual cone.

Under the first assumption of the model, the parameter β is the ratio of average crown length to tree spacing, $(H-H_C)/X$, in a closed stand. This ratio can be expressed in terms of a cotangent of an angle ϕ, i.e. $(\cot\phi)/2=(H-H_C)/X$ (Figure 1). The angle ϕ defines a cone with apex H around each tree. The intersection points of adjacent cones define the maximum average crown length that can exist, given the average spacing (see Figure 2). As the apex of a cone rises with H over time, the intersection points also rise. When an intersection point rises to the elevation of a crown base, the crown base begins to rise. Thinning and mortality from self-thinning increases the average spacing, which allows for longer crown lengths.

Modified crown-rise model

A fit of the original crown-rise model to spacing trial data (described below) yielded a diagonal trend in the graph of residuals versus initial spacing. The trend is eliminated by altering the first assumption of the original model from $H-H_C=\beta X$ to $(H-\alpha)-H_C=\beta X$. Hence, crown height is modelled by

$$H_C(t)=\max[\nu H(t),H_C(t-1),H(t)-\alpha-\beta X(t)]+\epsilon \quad (3)$$

The parameter β now is defined as the ratio of partial crown length to average spacing, $(H-\alpha-H_C)/X$, so the apices of the crown-length cones occur at height $H-\alpha$ instead of H.

A second modification to the original model provides for individualized crown heights. Let H_i be the height of the ith tree, and let H_{C_i} be the crown height, then

$$\begin{aligned}H_{C_i}(t)=\max\{&\nu H(t),H_{C_i}(t-1),H(t)-\alpha-\beta X(t)\\&+\gamma[H_i(t)-H(t)]\}+\epsilon_i\end{aligned} \quad (4)$$

With this second modification, individual crown base heights may occur above and below the stand average.

Methods

We fitted the original, modified and individualized crown-rise models with data from spacing trials maintained by the Forest Modeling Research Cooperative at Virginia Polytechnic Institute and State University. Based on a design by Lin and Morse (1975), the spacing trials comprise three replications of 16 different spacing patterns, resulting in 9 distinct densities (ranging from 747 to 6727 stems ha^{-1}) at each of four locations – Buckingham, Halifax and King and Queen Co., Virginia; and Halifax Co., North Carolina (Amateis *et al.*, 1988). The first two sites are located on the Piedmont plateau, the latter two on the coastal plain. The trials were initiated in 1983 and have spawned several recent reports (Amateis and Burkhart, 2012; Antón-Fernández *et al.*, 2012; Valentine *et al.*, 2012; VanderSchaaf and Burkhart, 2012).

The requisite data for our present purpose were gathered from ages 2 to 25 years. Observation sets comprising height, height of the crown base and stand density were measured yearly from age 2 to 10, then every other year to age 22, with a final measurement at age 25. Some plots were dropped from the study following an ice storm, others after a hurricane.

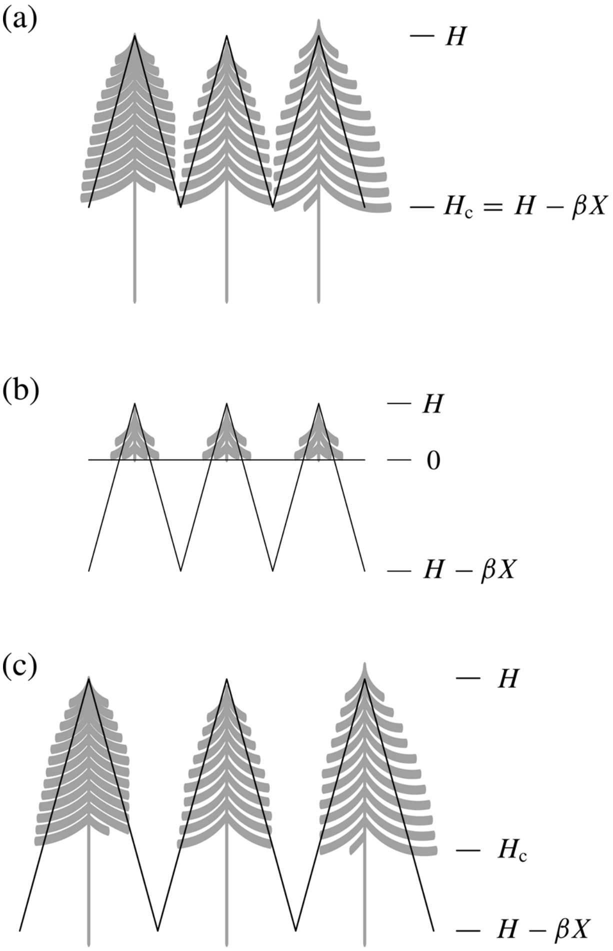

Figure 2 Crown-rise model for (a) closed, (b) recently planted and (c) thinned stands. Intersection points of the cones at elevation $H-\beta X$ define the maximum crown length, βX, given the spacing, X. Over time the intersection points rise with average tree height. When an intersection point rises to the base of a crown, the crown base begins to rise commensurate with H. Thinning and mortality from self-thinning increases the average spacing, which allows for longer crown lengths. Adapted from Valentine *et al.* (1994).

Table 1 Estimates of parameters of the linear crown-rise model, revised with a constant for loblolly pine

Parameter	Location	Estimate	SE	t-value	Pr(> |t|)
ν		0.1938	0.00381	50.8	<0.0001
α		1.4547	0.04073	89.5	<0.0001
β	1 and 2	1.6502	0.01843	78.4	<0.0001
	3 and 4	1.3367	0.01705	35.7	<0.0001

Table 2 Estimates of parameters of the individualized linear crown-rise model for loblolly pine

Parameter	Location	Estimate	SE	t-value	Pr(> |t|)
ν		0.1929	0.00335	57.6	<0.0001
α		1.4140	0.03633	102.3	<0.0001
β	1 and 2	1.6837	0.01645	89.8	<0.0001
	3 and 4	1.3670	0.01522	38.9	<0.0001
γ		0.3444	0.00814	42.3	<0.0001

We extracted a 1-in-15 systematic sample of observations sets from the overall data bank, which yielded 6619 observation sets, with no more than two observations per tree. We fit the crown-rise models in R by non-linear least squares. We also tested for differences in values of α and β among locations.

Results

The parameter estimates for model (3) and model (4), respectively, are provided in Tables 1 and 2. Of note, there is very little difference between the estimated values of ν, α and β for the two models, although the root-mean-square residual decreases from 0.75 m for model (3) to 0.67 m for model (4). Likewise, using Lorey's height or quadratic mean height instead of average height has almost no effect on the parameter estimates. Results for fits with these alternative heights and graphs of residuals versus predicted crown height, tree tip height, initial spacing and stand age (Supplementary Figure S1) are provided in Supplementary data.

The estimate of the ratio, β, differs between regions, indicating longer crowns, given the spacing, in the Piedmont region than in the coastal region. However, the region is confounded with the seed-sources of the planting stocks, so all we can conclude is that one set of parameters does not apply to all situations: If you have seen one loblolly stand, you have not seen them all.

The result that $\gamma > 0$ from the fit of (4) is consistent with what Sprugel (2002) called, "Milton's law of resource availability and allocation", which posits that the taller (shorter) trees should have the higher (lower) crown heights.

Example

We now demonstrate how one might use the modified crown-rise model to forecast time courses of the dbh, height and crown height of a 'mean tree' within an even-aged stand. We use a bridging model (Valentine and Mäkelä, 2005; Valentine *et al.*, 2012) to generate the forecasts. Besides the crown-rise model, the bridging model incorporates models that describe yearly changes in the tree's height and average spacing to model crown-length dynamics. In addition, a time-course of tree dbh and the development of the entire diameter profile of the central stem, except for the butt swell, is predicted from the crown-length dynamics.

Height growth rate is modelled by

$$\frac{\mathrm{d}H}{\mathrm{d}t} = g_1 L_c \frac{g_2 - g_4 H_c - L_c}{g_3 + g_5 H_c + L_c} \tag{5}$$

where $L_c = H - H_c$ (m) is average crown length (Valentine and Mäkelä, 2005). This height-growth model derives from a carbon balance, pipe model theory (Shinozaki *et al.*, 1964) and an optimal control model of crown allometry (Mäkelä and Sievänen, 1992). Height growth in loblolly pine is affected by both initial spacing (MacFarlane *et al.*, 2000) and thinning (Sharma *et al.*, 2006). This model accords with those findings, because the height growth rate is a function of crown length, which in turn is a function of spacing after closure; consequently, the height growth rate also responds to thinning. Other height growth models could substitute.

We assume that average spacing, X, is constant until crown height, H_c, rises to a height that is greater than the expected average tree height at closure, i.e. $H_{\text{close}} = \alpha + \beta X(0)$, where $X(0)$ is the initial spacing. Then we let spacing either slowly increase at the rate $u > 0$ (m year^{-1}) or remain constant ($u = 0$),

$$\frac{\mathrm{d}X}{\mathrm{d}t} = \begin{cases} 0, & H_c < \alpha + \beta X(0) \\ u, & \text{otherwise} \end{cases} \tag{6}$$

The effect of suppression on stem growth could be modelled by letting u take a negative value.

The rate of increase in the height of the crown base is modelled by the time derivative of (3), viz.,

$$\frac{\mathrm{d}H_c}{\mathrm{d}t} = \begin{cases} \nu \dfrac{\mathrm{d}H}{\mathrm{d}t}, & H_c > H - \alpha - \beta X \\ \dfrac{\mathrm{d}H}{\mathrm{d}t} - \beta \dfrac{\mathrm{d}X}{\mathrm{d}t}, & \text{otherwise} \end{cases} \tag{7}$$

Finally, we model the development of the stem profile of the mean tree. Let A_h^+ (cm^2) be the cross-sectional area at height h (m) on the central stem of a tree, and let L_h (m) be the vertical distance from the tip of the tree to h, i.e. $L_h = H - h$. Then, $\mathrm{d}L_h/\mathrm{d}t = \mathrm{d}H/\mathrm{d}t$ and $\mathrm{d}L_c/\mathrm{d}t = \mathrm{d}H/\mathrm{d}t - \mathrm{d}H_c/\mathrm{d}t$. The profile model is

$$\frac{\mathrm{d}A_h^+}{\mathrm{d}t} = \begin{cases} \beta_A z L_h^{z-1} \left((1+\eta) \dfrac{\mathrm{d}L_h}{\mathrm{d}t} \right), & L_h \le L_c \\ \beta_A z L_c^{z-1} \left(\dfrac{\mathrm{d}L_h}{\mathrm{d}t} + \eta \dfrac{\mathrm{d}L_c}{\mathrm{d}t} \right), & L_h > L_c \end{cases} \tag{8}$$

where β_A, η and z are parameters (Valentine *et al.*, 2012). A_h^+ takes an initial value of zero if h is greater than the tree's tip

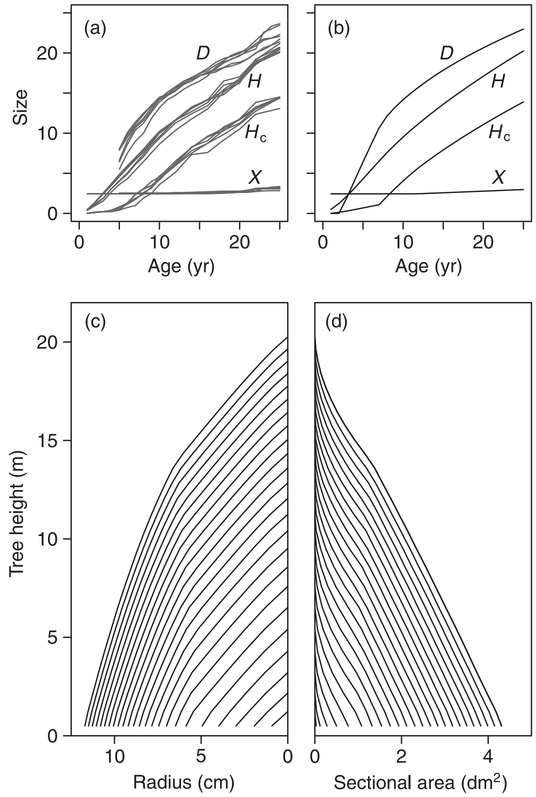

Figure 3 (a) Time-courses of tree averages from six research plots in spacing trial locations 3 and 4, with 2.44 m spacing (D, dbh (cm); H, height (m); H_c, crown height (m); X, spacing (m)); (b) mean-tree predictions from the bridging model; (c,d) predicted stem profiles of the mean tree from age 1 to 25 years.

height. Ordinarily, we are interested in cross-sectional growth at breast height, $h = b$, and at heights h_i ($i = 1, 2, \ldots, m$), where h_i is the height of the tree's ith annual node on the central stem. The expression, $1 + \eta$, may relate to the ratio of the specific volume – volume per unit dry mass – of crown wood to mature wood.

R code for the implementation of this mean-tree model, instructions and parameter values are provided in Supplementary data. Figure 3 depicts the results for a mean tree with an initial height of 0.4 m in a stand with 2.44 m spacing, with crown-rise parameter values for the coastal plain region.

Discussion

The crown-rise model is driven by the increase in average tree height and changes in spacing or stand density, information that is easily obtainable. The model is applicable where desired response variables such as dbh or whole-stem growth can be characterized in terms of crown-length dynamics, e.g. by CROBAS (Mäkelä, 1997) or, as demonstrated, by the related bridging model (Valentine and Mäkelä, 2005). Dean *et al.* (2013) describe an alternative approach to modelling stem growth from crown dynamics.

Fits of the original crown-rise model, (1), have returned estimates of $\hat{\beta} = 2.05$, 1.91 and 2.27, respectively, for loblolly pine in Eastern Texas (Valentine *et al.*, 1994), the coastal plain of Virginia and North Carolina and the Piedmont region of Virginia (this study). For the modified model, the estimate of β is significantly smaller for the coastal plain region than for the Piedmont region, though one estimate of the constant, α, applies in both regions. Whether differences result from acclimation to local edaphic and environmental conditions or to other causes is an open question.

Acclimation would require some degree of structural and functional plasticity. The result that the taller trees have higher crown-base heights within even-aged loblolly pine stands agrees with observations in stands of many species, and may be indicative of inherent plasticity. Sprugel (2002) contended that this is a case where resource availability is outweighed by resource allocation; carbon is invested where it is likely to have the best return, as measured in terms of carbon fixed per unit of biomass or nitrogen invested. Consequently, branches on suppressed trees continue to grow and produce new leaves at light levels where live branches on dominant trees do not occur, because resources are preferentially allocated elsewhere.

A bridging model is designed to provide a connection between a process-based model and practical application (Valentine and Mäkelä, 2005). The original bridging model of tree growth was 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 (1997; 2002), but with the explicit objective of simplicity in the formulation, which affords consolidation, resulting in an empirical model with relatively few parameters. We expect that the 'statistical fitness' of bridging models will evolve to provide better forecasts. In this regard, (7) and (8) can be considered improvements to the original bridging model.

Supplementary data

Supplementary data are available at *Forestry* Online.

References

Amateis, R.L. and Burkhart, H.E. 2012 Rotation-age results from a loblolly pine spacing trial. *South. J. Appl. For.* **36**, 11–18.

Amateis, R.L., Burkhart, H.E. and Zedaker, S.M. 1988 Experimental design and early analyses for a set of loblolly pine spacing trials. In *Forest Growth Modeling and Prediction*. A. Ek, S. Shifley and T. Burk (eds). Gen. Tech. Rep. NC-120. St Paul, Minnesota: Forest Service, North Central Experiment Station.

Antón-Fernández, C., Burkhart, H.E. and Amateis, R.L. 2012 Modeling the effects of initial spacing on stand basal area development of loblolly pine. *For. Sci.* **58**, 95–105.

Dean, T.J., Jerez, M. and Cao, Q.V. 2013 A simple stand growth model based on canopy dynamics and biomechanics. *For. Sci.* **59**, (in press). doi:10.5849/forsci.11-108.

Lin, C.H. and Morse, P.M. 1975 A compact design for spacing experiments. *Biometrics* **31**, 661–671.

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

Mäkelä, A. 1997 A carbon balance model of growth and self-pruning in trees based on structural relationships. *For. Sci.* **43**, 7–24.

Mäkelä, A. 2002 Derivation of stem taper from the pipe theory in a carbon balance framework. *Tree Physiol.* **22**, 891–905.

Mäkelä, A. and Sievänen, R. 1992 Height-growth strategies in opengrown trees. *J. Theor. Biol.* **159**, 443–467.

Pruves, D.W., Lichstein, J.W. and Pacala, S.W. 2007 Crown plasticity and competition for canopy space: a new spatially implicit model parameterized for 250 north american tree species. *PLoS One* **2**, e870.

Sharma, M., Smith, M., Burkhart, H.E. and Amateis, R.L. 2006 Modeling the impact of thinning on height development of dominant and codominant loblolly pine trees. *Ann. For. Sci.* **63**, 349–354.

Shinozaki, K., Yoda, K., Hozumi, K. and Kira, T. 1964 A quantitative analysis of plant form – the pipe model theory. ii. further evidence of the theory and its application in forest ecology. *Jpn. J. Ecol.* **14**, 133–139.

Sprugel, D.G. 2002 When branch autonomy fails: Milton's law of resource availability and allocation. *Tree Physiol.* **22**, 1119–1124.

Valentine, H.T., Herman, D.A., Gove, J.H., Hollinger, D.Y. and Solomon, D.S. 2000 initializing a model stand for process-based projection. *Tree Physiol.* **20**, 393–398.

Valentine, H.T., Ludlow, A.R. and Furnival, G.M. 1994 Modeling crown rise in even-aged stands of sitka spruce or loblolly pine. *For. Ecol. Manage.* **69**, 189–197.

Valentine, H.T. and Mäkelä, A. 2005 Bridging process-based and empirical approaches to modeling tree growth. *Tree Physiol.* **25**, 769–779.

Valentine, H.T., Mäkelä, A., Amateis, R.L., Mäkinen, H. and Ducey, M.J. 2012 Models relating stem growth to crown length dynamics: application to loblolly pine and norway spruce. *Trees* **26**, 469–478.

VanderSchaaf, C.L. and Burkhart, H.E. 2012 Development of planting density-specific density management diagrams for loblolly pine. *South. J. Appl. For.* **36**, 126–129.