

# Bridging process-based and empirical approaches to modeling tree growth

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**Summary** The gulf between process-based and empirical approaches to modeling tree growth may be bridged, in part, by the use of a common model. To this end, we have formulated a process-based model of tree growth that can be fitted and applied in an empirical mode. The growth model is grounded in pipe model theory and an optimal control model of crown development. Together, the pipe model and the optimal control model provide a framework for expressing the components of tree biomass in terms of three standard inventory variables: tree height, crown height and stem cross-sectional area. Growth rates of the inventory variables and the components of biomass are formulated from a carbon balance. Fundamentally, the parameters of the model comprise physiological rates and morphological ratios. In principle, the values of these parameters may be estimated by lower-level process models. Alternatively, the physiological and morphological parameters combine, under reasonable assumptions, into a set of aggregate parameters, whose values can be estimated from inventory data with a statistical fitting procedure.

*Keywords:* carbon balance, crown length, crown rise, diameter, height, optimal control model, pipe model, self-thinning.

## Introduction

The problem of forecasting tree growth can be approached as a problem in forecasting the assimilation and allocation of carbon and other constituents. Tree-level models of carbon allocation translate rates of carbon assimilation into growth rates of tree diameters, heights, volumes and other attributes. By providing these translations, allocation models link the sciences that underlie forestry to the goods and services that emerge from forestry.

Le Roux et al. (2001) recently reviewed 27 carbon-based models of tree growth, including their approaches to carbon allocation. Nearly half the models incorporate a “functional balance approach” to allocation. Two early examples of this approach (Valentine 1985, Mäkelä 1986) were grounded in pipe model theory (Shinozaki et al. 1964a, 1964b) and the principle of functional balance (Davidson 1969), but other ar-

chitectural rules can be added or substituted (see Le Roux et al. 2001, Table V). For example, an optimal control model of carbon allocation (Mäkelä and Sievänen 1992), which derives in part from pipe model theory and functional balance, has been incorporated into the CROBAS model (Mäkelä 1997).

The functional balance approach is one of four basic approaches listed by Le Roux et al. (2001) for modeling carbon allocation. By contrast, hundreds of empirical models of forest growth have been fitted, and they come in a rich, but somewhat frustrating, variety of mathematical forms. This variety may be due to the absence of a robust theory that affords the derivation of efficacious models with wide applicability. Commonly, one modeler may estimate one set of parameters, while another modeler, somewhere else, estimates a completely different set, perhaps for the same species. For example, Robinson and Ek (2000) noted the existence of seven growth models for red pine (*Pinus resinosa* Ait.) in one region. This is not an efficient strategy for attaining *lux et veritas*, nor one that takes advantage of fundamental biological knowledge and our most cogent theories and principles.

The theories and principles that underlie the functional balance approach to modeling allocation can also be used to formulate empirical models of tree growth. To substantiate this claim, we have formulated a simple carbon-based model of tree growth that can be fitted as an empirical model. Of necessity, the model incorporates minimal, rather than detailed, levels of structure and function and uses state variables that ordinarily are monitored in forest inventories: stem cross-sectional area (or diameter), height and crown height (or crown ratio).

The carbon-based model closely resembles CROBAS (Mäkelä 1997). The values of the parameters of the model can be specified by measuring or estimating physiological rates and morphological ratios or they can be supplied by lower-level process models. The latter procedure would normally apply when the model is used in a process-based framework for exploration, description or hypothesis generation. Alternatively, the physiological and morphological parameters can be combined into an identifiable set of aggregate parameters, whose values can be estimated from inventory data with a statistical fitting procedure. This is the normal procedure in forestry for

updating a past inventory to the present or projecting a present inventory into the future. The model also offers some middle ground, i.e., some hybridization between the two procedures.

Whether there is any advantage to using the same basic model in process-based and empirical modes is an open question. But any movement toward a common model seems sure to increase communication between the two schools of thought. The approach may also afford a gradual transition from empirical to process-based models, especially in regions where mixed stands contain numerous species. Most importantly, the empirical model provides an upper bound on acceptable error. If forecasts from a process-based model have greater error than the empirical model, then there is little reason to apply the former to problems that can be addressed by either.

We begin with some essential definitions, and then we formulate the model. Symbols are listed in Table 1.

### Definitions

Let  $H$  (m) be tree height and let  $H_C$  be crown height, i.e., the height of the base of the live crown. An increase in  $H_C$  over time is called crown rise. Crown length ( $L_C$ ; Figure 1) is:

$$L_C = H - H_C \quad (1)$$

The growth rate of crown length ( $\text{m year}^{-1}$ ) equals the growth rate of tree height less the rate of crown rise, i.e.,

$$\frac{dL_C}{dt} = \frac{dH}{dt} - \frac{dH_C}{dt} \quad (2)$$

Ignoring bark, let  $A^+(h)$  ( $\text{m}^2$ ) be the total cross-sectional area of a stem at any height  $h$  (m) between the ground line,  $h = 0$ , and the crown base,  $h = H_C$  (if  $h =$  breast height,  $A^+(h)$  is equivalent to the forester's definition of basal area inside bark). Dividing the total cross-sectional area into components, let  $A(h)$  be the cross-sectional area of sapwood at  $h$  and let  $A^-(h)$  be the cross-sectional area of heartwood, a term we use in a generic sense to describe any type of non-conducting xylem. Focusing on the sapwood area, we note that:

$$A(h) = A^+(h) - A^-(h) \quad (3)$$

The growth rate of the total cross-sectional area,  $dA^+(h)/dt$  ( $\text{m}^2 \text{ year}^{-1}$ ), is equivalent to the rate of production of new sapwood area, and the growth rate of heartwood area,  $dA^-(h)/dt$ , is equivalent to the rate of senescence of old sapwood area. Thus, the growth rate of sapwood area is:

$$\frac{dA(h)}{dt} = \frac{dA^+(h)}{dt} - \frac{dA^-(h)}{dt} \quad (4)$$

Let  $W$  (kg C) be the live biomass of a tree. We divide this live biomass into three components: foliage ( $W_F$ ), fine roots ( $W_R$ ) and live woody tissues, principally sapwood ( $W_W$ ), i.e.,

$$W = W_F + W_R + W_W \quad (5)$$

We denote the growth rate of a component of biomass ( $\text{kg C year}^{-1}$ ) by  $dW_i/dt$  ( $i = F, R, W$ ), the rate of production of new biomass by  $dW_i^+/dt$  and the rate of transition of live biomass to dead biomass by  $dW_i^-/dt$ . In the case of woody biomass, the

Table 1. Variables and parameters.

Symbol	Definition	Units
$A(h)$	Cross-sectional area of sapwood at height $h$	$\text{m}^2$
$A^+(h)$	Cross-sectional area inside bark at height $h$	$\text{m}^2$
$A^-(h)$	Cross-sectional area of heartwood at height $h$	$\text{m}^2$
$A_C$	Cross-sectional area of sapwood at the crown base	$\text{m}^2$
$C$	Crown coverage	$\text{m}^2 \text{ m}^{-2}$
$G$	Cross-sectional area of stem at breast height	$\text{m}^2$
$H$	Tree height	m
$H_C$	Crown height	m
$L_C$	Crown length	m
$W_B$	Live woody biomass in branches	kg C
$W_{B+S}$	Live woody biomass aboveground	kg C
$W_C$	Live woody biomass above the crown base	kg C
$W_F$	Foliage biomass	kg C
$W_R$	Feeder root biomass	kg C
$W_S$	Live woody biomass in main stem	kg C
$W_W$	Live woody biomass above and below ground	kg C
$W_X$	Heartwood biomass	kg C
$W_i^+$	Cumulative production of $W_i$ , $i = F, R, W$	kg C
$W_i^-$	Cumulative senescence of $W_i$ , $i = F, R, W$	kg C
$c$	Overhead cost of converting photosynthate to biomass	$\text{kg C (kg C)}^{-1}$
$m_i$	Specific rate of maintenance respiration of $W_i$ , $i = F, R, W$	$\text{kg C (kg C year)}^{-1}$
$s, s_0$	Specific rate of photosynthesis	$\text{kg C (kg C year)}^{-1}$
$s_1$	Decrease in $s$ per unit tree height (hydraulic limitation)	$\text{kg C (kg C m year)}^{-1}$
$z$	Ratio of specific growth rates: sapwood area to crown length	–
$\alpha$	Crown intersection angle	°
$\beta_0$	Ratio of total to aboveground live woody biomass	$\text{kg C (kg C)}^{-1}$
$\beta_B$	Ratio of mean branch length to crown length	$\text{m m}^{-1}$
$\beta_S$	Ratio of mean pipe length in main stem of crown to crown length	$\text{m m}^{-1}$
$\varepsilon$	Net production per unit of photosynthate (constant efficiency)	$\text{kg C (kg C)}^{-1}$
$\nu_F$	Leaf longevity	years
$\nu_R$	Feeder root longevity	years
$\rho_F$	Ratio of foliage mass to cross-sectional area of sapwood	$\text{kg C m}^{-2}$
$\rho_R$	Ratio of feeder root mass to cross-sectional area of sapwood	$\text{kg C m}^{-2}$
$\rho_W$	Wood density	$\text{kg C m}^{-3}$

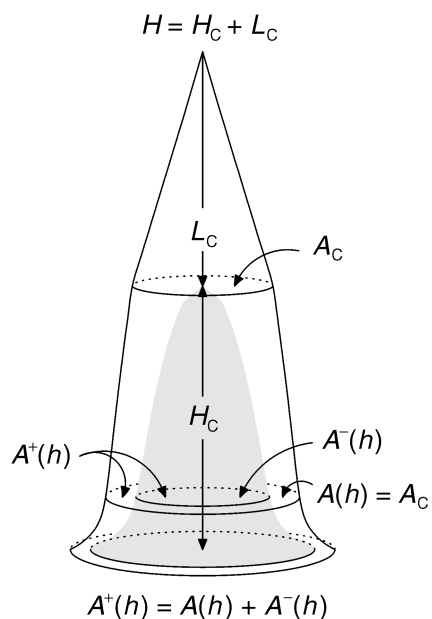


Figure 1. Defined lengths and cross-sectional areas of the main stem of a tree. Heartwood is shaded.

transition of live to dead biomass includes the conversion of sapwood to heartwood. Therefore:

$$\frac{dW}{dt} = \sum_i \frac{dW_i}{dt} \quad (6)$$

where:

$$\frac{dW_i}{dt} = \frac{dW_i^+}{dt} - \frac{dW_i^-}{dt} \quad (7)$$

### Structure

Observed consistencies in structural relationships among species have given rise to theories of tree structure that apply rather generally. In particular, the pipe model theory of stem form (Shinozaki et al. 1964a, 1964b) is based on observations of an approximately constant ratio between the sapwood cross-sectional area at the base of a stem or branch and the total mass of foliage borne by that stem or branch. Implicit in this assumption of a constant ratio is the notion of area-preserving branching (also known as Leonardo's rule), where the cross-sectional areas of daughter branches sum to approximate the cross-sectional area of the mother branch. Even more important for our purposes is a central idea of pipe model theory: that sapwood cross-sectional area is preserved at branchings and constant at all heights between the crown base and the ground line. The pipe model is also applicable to coarse roots (e.g., Carson and Harrington 1987, Richardson and zu Dohna 2003). In addition, an approximately constant ratio of fine root mass to coarse root sapwood area has been found in stands of Scots pine (*Pinus sylvestris* L.) (Vanninen and Mäkelä 1999). In concert with the principle of functional balance, this ratio decreases from poor to good sites.

The pipe model does not account for butt swell or buttresses. And, in disagreement with the theory, sapwood area is not constant between the base of the crown and the ground line, but reportedly waxes and wanes (e.g., Waring et al. 1982). Nevertheless, for our purposes, an assumption of constant sapwood area is reasonable if the sapwood area averaged over the length of the bole approximates the sapwood area at the base of the crown.

### Biomass

Among other things, pipe model theory allows us to express the components of live biomass in terms of sapwood area, tree height and crown height. Mäkelä (1986, 1997) noted that the mass of foliage supported by a unit of sapwood cross-sectional area varies according to whether the sapwood is in a branch, the main stem, or a coarse root. We shall ignore the slight difference between branches and the main stem. Focusing on the main stem at the crown base, the mass of foliage is approximated by:

$$W_F \doteq \rho_F A_C \quad (8)$$

where  $A_C$  is sapwood area at the crown base, i.e.,  $A_C \equiv A(H_C)$  and  $\rho_F$  is the ratio of foliage mass to cross-sectional area of sapwood. We assume, generally, that fine root mass is proportional to foliage mass, so:

$$W_R \doteq \rho_R A_C \quad (9)$$

where  $\rho_R$  is the ratio of feeder root mass to the cross-sectional area of sapwood, and  $\rho_F$  and  $\rho_R$  have dimensions  $\text{kg C m}^{-2}$ .

To express live woody biomass in terms of  $A_C$ ,  $H$  and  $H_C$ , we must first express the mean length (m) of a sapwood pipe in terms of  $H$  and  $H_C$ . In accordance with pipe model theory, the mean pipe length in the main stem is equivalent to the crown height plus  $\beta_S L_C$  ( $0 < \beta_S < 1$ ), i.e., the distance from the crown base to a point within the crown where half the sapwood area has branched off from the main stem. Hence, mean pipe length in the central main stem is:

$$H_C + \beta_S(H - H_C) \equiv H_C + \beta_S L_C \quad (10)$$

In the absence of heartwood above the crown base,  $\beta_S \approx 1 - \sqrt{1/2} \approx 0.293$  if the shape of the main stem above the crown base approximates a cone;  $\beta_S \approx 1/2$  if the shape approximates a quadratic paraboloid. If heartwood occurs above the crown base,  $\beta_S$  is a larger fraction than otherwise.

We assume that the mean pipe length through a branch off the main stem is:

$$\beta_B(H - H_C) \equiv \beta_B L_C \quad (11)$$

In connection with the study reported by Valentine et al. (1994), randomized branch sampling for mean pipe length in 30 loblolly pine trees, selected from among 9 stands, furnished  $\beta_B + \beta_S = 0.77$ .

Denoting the carbon density of the wood by  $\rho_W$  ( $\text{kg C m}^{-3}$ ), the live woody biomass in branches ( $W_B$ ) is approximated by:

$$W_B \doteq \rho_W \beta_B A_C L_C \quad (12)$$

and the live woody biomass in the central main stem ( $W_S$ ) is approximated by:

$$W_S \doteq \rho_W A_C (H_C + \beta_S L_C) \quad (13)$$

provided the central stem extends to the tree tip. The live woody biomass above the crown base ( $W_C$ ) is approximated by:

$$W_C \doteq \rho_W (\beta_B + \beta_S) A_C L_C \quad (14)$$

and the aboveground live woody biomass ( $W_{B+S}$ ) is approximated by:

$$W_{B+S} \doteq \rho_W A_C (H_C + (\beta_B + \beta_S) L_C) \quad (15)$$

We assume that the mass of below ground sapwood is proportional to the amount above ground. Let  $\beta_0$  be the ratio of total sapwood to aboveground sapwood; then the mass of total sapwood is approximated by:

$$W_W \doteq \rho_W A_C (\beta_1 H + \beta_2 H_C) \quad (16)$$

where  $\beta_1 = \beta_0(\beta_B + \beta_S)$  and  $\beta_2 = \beta_0 - \beta_1$ .

Equations 12–16 are alternatives to allometric models for estimating of sapwood mass or volume and can be fitted to suitable data, which would provide estimates of  $\beta_B$ ,  $\beta_S$ ,  $\beta_{B+S}$ ,  $\beta_1$  and  $\beta_2$ . These models may be most useful in studies of sapwood respiration and carbon sequestration. A formula for approximating the mass of heartwood ( $W_X$ ) is provided in the next section. The total woody biomass in a tree ( $\text{kg C}$ ) is approximated by  $W_W + W_X$ .

### Cross-sectional growth

The structural model quantifies the live biomass of a tree in terms of three state variables,  $A_C$ ,  $H$  and  $H_C$ . In this section, we express the growth of  $A_C$  in terms of the growth of  $H$  and  $H_C$ . We also formulate growth models for total cross-sectional area below crown,  $A^+(h)$ , and heartwood cross-sectional area below crown,  $A^-(h)$ . To do this, we utilize an allometric relationship between crown length and cross-sectional area that has been found to characterize tree form.

Mäkelä and Sievänen (1992) formulated an optimal control model, based on an evolutionary argument, that relates foliage mass to crown length as:

$$W_F \propto L_C^z \quad (17)$$

Under the assumptions of pipe model theory,  $W_F \propto A_C$ , so under the combined assumptions of pipe model theory and the optimal control model:

$$A_C \propto L_C^z \quad (18)$$

assuming that  $A(h) \equiv A_C$  for  $0 \leq h \leq H_C$ :

$$A(h) = \beta_3 L_C^z \quad (19)$$

where  $\beta_3$  is a coefficient of proportionality.

If quarter-power scaling is accurate for tree crowns, then  $z = 3$  (e.g., West et al. 1999). Empirical fits of Equation 17, however, suggest that  $z$  is ordinarily less than 3. Mäkelä and Sievänen observed  $z = 2.4$  for open-grown Scots pine, and  $z < 3$  has been consistently estimated for different boreal species (Figure 2).

Equations 8 and 18 relate properties of the whole crown to the cross-sectional area at the crown base. From the optimal control model and the pipe model, we may hypothesize that

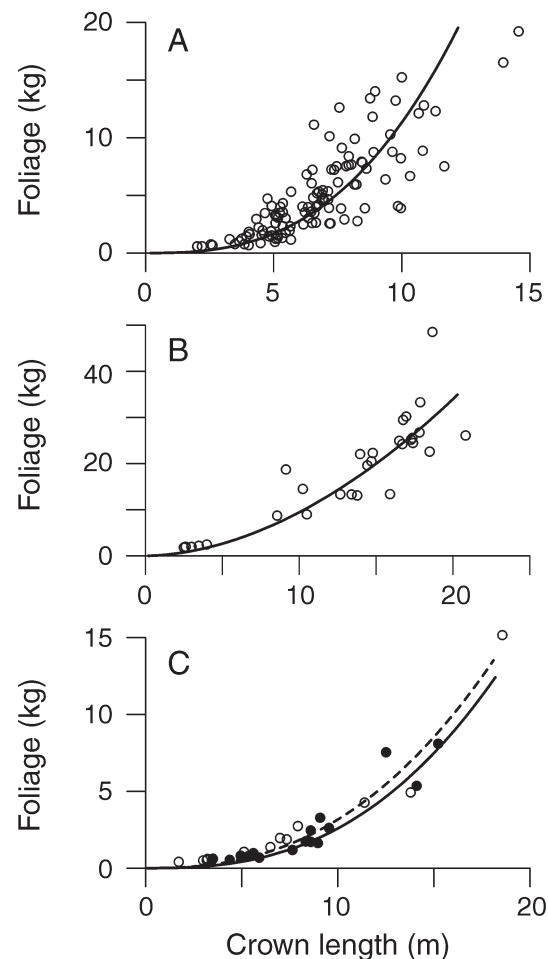


Figure 2. Foliage mass as a function of crown length. (A) Scots pine (*Pinus sylvestris*):  $W_F = 0.0201L_C^{2.75}$ ,  $R^2 = 0.76$ ,  $n = 119$  (trees from 17 stands of variable age, site type and density (Vanninen 2003)); (B) Norway spruce (*Picea abies* (L.) Karst):  $W_F = 0.133L_C^{1.85}$ ,  $R^2 = 0.95$ ,  $n = 29$  (trees from five stands of variable age and density (Kantola and Mäkelä 2004)); (C) silver birch (*Betula pendula* Roth.) filled circles, solid line:  $W_F = 0.0062L_C^{2.62}$ ,  $R^2 = 0.93$ ,  $n = 18$  (trees from three stands of equal age and variable density, Ilomäki et al. 2003), open circles, dashed line:  $W_F = 0.012L_C^{2.45}$ ,  $R^2 = 0.98$ ,  $n = 12$  (dominant trees from six stands differing in age (Parviainen 1999)).

Equations 17 and 18 apply at any point above the crown base on the main stem. In that case, the relationship:

$$A^*(l) \propto l^z \quad (20)$$

would define the taper of the main stem inside the crown, where  $A^*(l)$  is sapwood cross-sectional area of the main stem at a distance  $l$  from the tip. This relationship would also provide a value for  $\beta_5$  and it would render thousands of observations of stem taper gathered over the last two centuries (e.g., Gray 1943, Assmann 1970) a basis for estimating the value of  $z$  for different species (Appendix 1). Such models suggest that  $z \leq 2$  is not unusual. For example, the taper model of Valentine and Gregoire (2001) yields values between 1.4 and 2.2 for four North American species (Figure 3). However, estimates based on foliage and sapwood suggest that  $z$  may vary somewhat from the top to the bottom of a crown (Kershaw and Maguire 2000, Mäkelä and Vanninen 2001, Kantola and Mäkelä 2004). Hence, if  $z$  is estimated from taper data with Equation 20, it may be best to use data from the lower half of the crown, since we are most interested in the relationship between  $L_C$  and  $A_C$ , i.e., Equation 19.

For the derivation of the cross-sectional growth model, the critical value of  $z$  is that which obtains for Equation 19. The time derivative of Equation 19 expresses the growth rate of  $A(h)$  in terms of the growth rate of crown length, i.e.,

$$\frac{dA(h)}{dt} = z \left( \frac{A(h)}{L_C} \right) \frac{dL_C}{dt} \quad (21)$$

or, substituting Equations 2 and 4 into Equation 21:

$$\frac{dA^+(h)}{dt} - \frac{dA^-(h)}{dt} = z \left( \frac{A^+(h) - A^-(h)}{H - H_C} \right) \left( \frac{dH}{dt} - \frac{dH_C}{dt} \right) \quad (22)$$

We decompose the growth rate of  $A(h)$  into a rate of production of new sapwood cross-sectional area:

$$\frac{dA^+(h)}{dt} = z \left( \frac{A^+(h) - A^-(h)}{H - H_C} \right) \frac{dH}{dt} \quad (23)$$

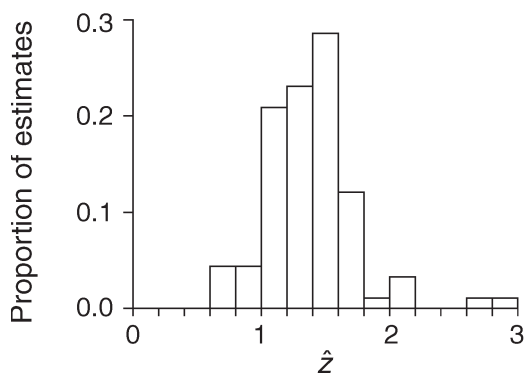


Figure 3. Estimates of  $z$  calculated from two within-crown measurements (i.e., mid-crown and crown base) from each of 91 slash pines (*Pinus elliotii* Engl.) (Valentine and Gregoire 2001).

and a rate of conversion of old sapwood cross-sectional area into new heartwood cross-sectional area:

$$\frac{dA^-(h)}{dt} = z \left( \frac{A^+(h) - A^-(h)}{H - H_C} \right) \frac{dH_C}{dt} \quad (24)$$

Note that Equation 22 equals Equation 23 minus Equation 24. This decomposition accords with our assumptions to this point, because Equation 23 indicates that the rate of production of new sapwood area is related to growth rate of height, and Equation 24 indicates that the rate of conversion of old sapwood area to new heartwood area is related to the rate of crown rise. In concert with this model, Kaipianen and Hari (1985) found good agreement between the number of sapwood rings and the number of live whorls in Scots pine.

Integration of Equations 22–24 from year  $t_1$  to year  $t_2$  provides cross-sectional growth from year  $t_1$  to year  $t_2$ , given the growth in both crown height and total height (Figure 4). For example, Equation 24 integrates from year  $t_1$  to year  $t_2$  to give a new heartwood cross-sectional area, given a new crown height, i.e.,

$$A_{t_2}^-(h) = A_{t_1}^+(h) - A_{t_1}^-(h) \left( \frac{H_{t_1} - H_{C,t_2}}{L_{C,t_1}} \right)^z \quad (25)$$

Note that if  $H_{C,t_2}$  equals  $H_{C,t_1}$ , there is no growth of heartwood cross-sectional area.

Equation 22 integrates from year  $t_1$  to year  $t_2$  to give new sapwood cross-sectional area, given the new tree height and crown height, i.e.,

$$A_{t_2}^+(h) = A_{t_1}^+(h) \left( \frac{L_{C,t_2}}{L_{C,t_1}} \right)^z \quad (26)$$

The new total cross-sectional area at height  $h$  is  $A_{t_2}^+(h) = A_{t_2}^+(h) + A_{t_2}^-(h)$ , or:

$$A_{t_2}^+(h) = A_{t_1}^+(h) + A_{t_1}^-(h) \left( \left( \frac{L_{C,t_2}}{L_{C,t_1}} \right)^z - \left( \frac{H_{t_1} - H_{C,t_2}}{L_{C,t_1}} \right)^z \right) \quad (27)$$

An accurate model of stem taper could be used to estimate  $z$  and initialize  $A(h) = A_C$ . Alternatively, we can eliminate  $A(h)$  from the model. From Equation 19, we note that  $A(h)/L_C^z$  equals a coefficient of proportionality,  $\beta_3$ . Let  $G$  be cross-sectional area at breast height, then Equation 27 can be rewritten as:

$$G_{t_2} = G_{t_1} + \beta_3 (L_{C,t_2}^z - (H_{t_1} - H_{C,t_2})^z) \quad (28)$$

We suggest fitting Equation 28 as a mixed-effects model, because  $\beta_3$  and  $z$  may vary from tree to tree.

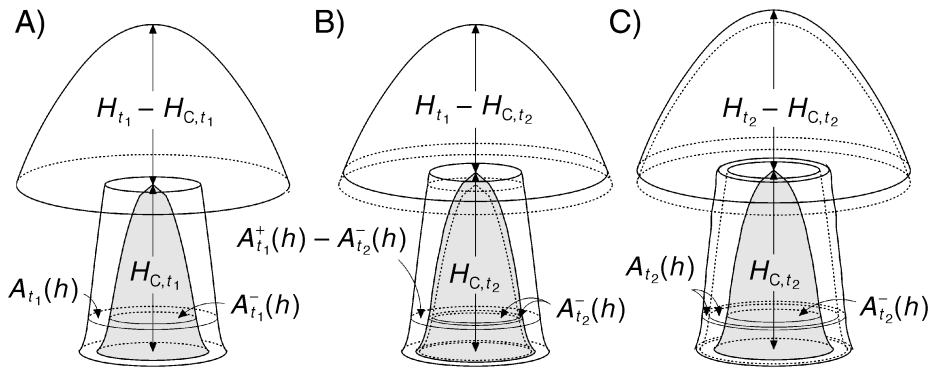


Figure 4. Cross-sectional growth. (A) The state of the model tree at the end of year  $t_1$ . (B) Heartwood (shaded area in figure) cross-sectional area at height  $h$  increases with crown height in a discrete jump at the start of year  $t_2$ . Sapwood cross-sectional area at this point in time is:  $A_{t_1}^+(h) - A_{t_1}^-(h) \propto (H_{t_1} - H_{C,t_2})^z$ . (C) Sapwood cross-sectional area increases with height growth in year  $t_2$ . The cross-sectional area of the growth ring is:  $A_{t_2}^+(h) - A_{t_1}^+(h)$ .

In principle, we may keep track of  $A_i^+(h)$  at several heights ( $h = h_1, h_2, \dots, h_n$ ). Equation 27 applies for each  $h_j$ . We may start to keep track of cross-sectional area at  $H_C$  in any year,  $t$ , that crown rise occurs, because under our assumptions:

$$A^+(H_C) = A_C \quad (29)$$

Thus, the model can provide a dynamic picture of the development of the bole profile. However, the model would not account for butt swell.

The volume ( $V$ ) of the bole, from the ground line to the crown base, can be approximated with Smalian's (trapezoidal) formula:

$$V = \sum_j^{n-1} \frac{A^+(h_j) + A^+(h_{j+1})}{2} (h_{j+1} - h_j) \quad (30)$$

The biomass in heartwood,  $W_X$  (kg C), is approximated by:

$$W_X \doteq \rho_W (V - A_C H_C) \quad (31)$$

### Height growth

The rate at which cross-sectional area accrues in Equations 27–28 depends on the growth rate of tree height. Fundamentally, this rate depends on the rates of photosynthesis and respiration.

By definition, the rate of production of live biomass is:

$$\sum_{i=F,R,W} \frac{dW_i^+}{dt} = P - R \doteq P - R_C - R_M \quad (32)$$

where  $P$  is the rate of photosynthesis by the tree,  $R \equiv R_C + R_M$  is the rate of total respiration,  $R_M$  is the rate of maintenance respiration and  $R_C$  is the rate of construction respiration. Equation 32 can be called a "carbon balance," since all of the components of this equation have dimensions ( $\text{kg C year}^{-1}$ ).

We define  $P = sW_F$ ,  $R_C = c \sum_i (dW_i^+/dt)$  and  $R_M = \sum_i (m_i W_i)$ , where  $s$  ( $\text{kg C (kg C year)}^{-1}$ ) is the specific rate of photosynthesis,  $c$  ( $\text{kg C (kg C)}^{-1}$ ) is the amount of photosynthate consumed in respiration per unit of new production, and  $m_i$  ( $\text{kg C (kg C year)}^{-1}$ ) is the specific rate of maintenance respiration

of  $W_i$ . To invoke an effect of hydraulic limitation on the rate of photosynthesis (e.g., Yoder et al. 1994), we assume that the specific rate of photosynthesis,  $s$ , decreases as a function of tree height, i.e.,

$$s = s_0 - s_1 H \quad (33)$$

where  $s_0$  has dimensions  $\text{kg C (kg C year)}^{-1}$  and  $s_1$  has dimensions  $\text{kg C (kg C year m)}^{-1}$ . Substituting into Equation 32,

$$\sum_i \frac{dW_i^+}{dt} = \frac{(s_0 - s_1 H) W_F - \sum_i m_i W_i}{1 + c} \quad (34)$$

Equation 34 allows for the popular simplifying assumption of "constant efficiency," where the ratio of total respiration to photosynthesis is constant, i.e.,  $R/P = 1 - \epsilon$ , where  $0 < \epsilon < 1$  (e.g., Landsberg and Waring 1997). This is the same as assuming that net production is proportional to photosynthesis, i.e.,  $P - R = \epsilon P$ . The "constant efficiency model" can be implemented from the full model, Equation 34, by setting  $m_i$  to 0 and  $c$  to  $(1 - \epsilon)/\epsilon$  (Mäkelä and Valentine 2001). This yields:

$$\sum_i \frac{dW_i^+}{dt} = \epsilon (s_0 - s_1 H) W_F \quad (35)$$

Equation 34 quantifies a tree's contribution to the net primary production of a stand; it is an appropriate starting point for the derivation of growth models for nearly all the tree attributes of interest to foresters. To obtain a height growth model, we can express each  $W_i$  and  $dW_i^+/dt$  in terms of  $H$ ,  $H_C$ ,  $A_C$  and their rates of change; substitute into Equation 34; and then solve for the growth rate of tree height. The details of the calculations for the following model are provided in the Appendix. It turns out that, under our assumptions, the growth rate of tree height is a function of tree height and crown height, i.e.,

$$\frac{dH}{dt} = g_1 (H - H_C) \left( \frac{g_2 - (g_4 - 1) H_C - H}{g_3 + (g_5 - 1) H_C + H} \right) \quad (36)$$

where  $g_1$ – $g_5$  are combinations of the structural and physiological parameters (see Appendix). Under the constant efficiency assumption,  $g_4 = 1$ , so  $g_2$  is asymptotic tree height.

Note that the growth rate of height is proportional to crown length. This formulation, in concert with a model of crown rise, captures competition effects of neighboring trees and forecasts the differentiation of tree heights, including overtopping and consequent self-thinning.

For the purpose of integration, we find it useful to rewrite the model thus:

$$\frac{dL_C}{dt} + \frac{dH_C}{dt} = g_1 L_C \left( \frac{g_2 - g_4 H_C - L_C}{g_3 + g_5 H_C + L_C} \right) \quad (37)$$

Prior to the onset of crown rise,  $H_C$  and  $dH_C/dt$  equal 0, so  $L_C$  is equivalent to tree height. Hence, integration of Equation 37 from  $t_1$  to  $t_2$  yields a growth model of tree height. After the onset of crown rise, we can integrate the model from  $t_1$  to  $t_2$  if we assume that  $H_C$  is constant over this period. Because  $H_C$  is assumed constant,  $dH_C/dt$  equals 0, so the integration yields a growth model for crown length. Our theory and assumptions furnish a growth model that is nonlinear in  $L_C$ , i.e.,

$$\frac{(\lambda - L_{C,t_2})^{1+\eta}}{L_{C,t_2}^\eta} = \Omega \exp(-g_1(t_2 - t_1)) \quad (38)$$

where:

$$\Omega = \frac{(\lambda - (H_{t_1} - H_{C,t_2}))^{1+\eta}}{(H_{t_1} - H_{C,t_2})^\eta} \quad (39)$$

$$\lambda = g_2 - g_4 H_{C,t_2} \quad (40)$$

$$\eta = \frac{g_3 + g_5 H_{C,t_2}}{\lambda} \quad (41)$$

We solve Equation 38 for  $L_{C,t_2}$  by iterative bisection, where  $H_{t_2} = L_{C,t_2} + H_{C,t_2}$ . If we set  $\eta = 0$ , the resultant equation provides an upper bound for the solution of Equation 38, i.e.,

$$L_{C,t_2}^* = \lambda - (\lambda - (H_{t_1} - H_{C,t_2})) \exp(-g_1(t_2 - t_1)) \quad (42)$$

Thus, the solution of Equation 38 is bracketed by  $[L_{C,t_1}, L_{C,t_2}^*]$ .

### Crown rise

Above, we have derived growth equations for cross-sectional area and height on the basis of structural consistencies and the carbon balance of the tree. To complete the model, we need to provide equations for crown rise. Unlike other variables in the model, the height of the crown base is not related solely to other structural variables in the model, as it is also strongly influenced by external factors, principally shading and physical crowding by other crowns.

Physical crowding affords wind-induced abrasion, which

destroys new growth, regardless of shade effects (e.g., Mitchell 1975). How shading induces crown rise remains an open question (Sprugel 2002), though leaves cannot grow where the light availability is too low. The theory of branch autonomy suggests that each branch is an independent unit that dies when its carbon balance turns from positive to negative (Sprugel et al. 1991). The principle of correlative inhibition assumes similar regulation by light but accounts for plasticity in leaf form and presentation, explaining why leaves are initiated under considerable shade, e.g., in a layered canopy (Snow 1931, Sprugel 2002). Some theories maintain that the crown as a whole influences each branch to maximize the carbon gain of the whole tree, leading not only to plasticity but also to evolutionarily stable adaptations that involve competition with neighbors (Nikinmaa and Hari 1990, Nikinmaa et al. 2004). This could explain why leaf initiation is inhibited in the lower crown if rapid height growth and increasing shading by other trees are underway, even though the light availability would momentarily support branch growth (Nikinmaa et al. 2004).

Empirical models of crown rise are usually constructed under the assumption that physical space is limiting (e.g., Mitchell 1975), whereas the few process-based models that model crown rise tend to use relationships based on light availability (e.g., Nikinmaa and Hari 1990). The two are closely related. Under the assumptions of our model, the relationship between crowding and light derives from (a) the allometric equation, Equation 17, and (b) the assumption that crown width is proportional to crown length, which relates crown projected area to foliage mass. The relationship is most apparent when  $z = 2$ , implying that stand foliage mass is proportional to crown coverage. If  $z < 2$ , increasing crown size will decrease foliage mass relative to crown coverage, and if  $z > 2$ , the opposite is true. The degree of shade cast by the crowns depends on the shade area of the crown, a combination of crown dimensions and foliage density (Oker-Blom et al. 1989). This suggests that limitations to shoot growth caused by crowding or shading are not easily distinguishable, and that models based on either could provide equally good results.

The stand-level crown-rise model of Valentine et al. (1992) assumes that crown height is constant across the stand, i.e.,

$$\bar{H}_{C,t_2} = \max \left( 0, \bar{H}_{C,t_1}, \bar{H}_{t_1} - \frac{\bar{D}_{t_1}}{2 \tan \alpha} \right) \quad (43)$$

where the overbars signify stand means and  $\bar{D}$  is mean inter-tree distance. This model has been adapted to apply to individual trees (Valentine et al. 2000); it requires a stem map, but has just one parameter in the form of an angle  $\alpha$  (Figure 5).

In CROBAS (Mäkelä 1997), the rate of crown rise, instead of crown height itself, is a function of crown coverage. It is defined through carbon allocation, increasing crown coverage shifting it from foliage growth to crown rise. If crown coverage is defined separately at each horizontal level of the canopy, this model can also be applied to a stand consisting of distance-independent size classes, resulting in different crown heights for trees of different size (Mäkelä et al. 2000). Whereas the crown

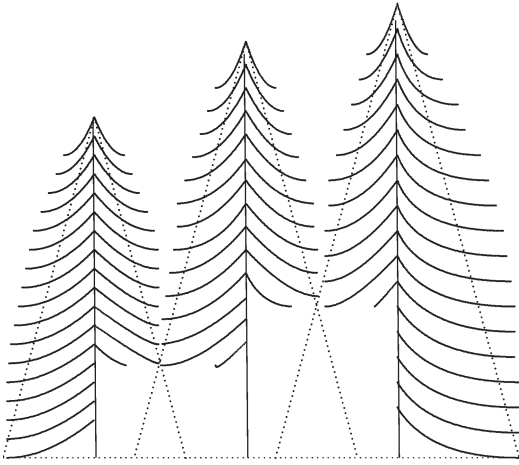


Figure 5. Crown rise can be modeled mechanically with one parameter in the form of an angle. The dotted lines form the angle  $\alpha$  with the main stems. Intersection points, which define crown heights, rise with increasing tree height (see Valentine et al. 2000).

rise model of Valentine et al. (1992) may be interpreted in terms of direct regulation by light (or physical space), CRO-BAS combines these with some degree of control by the tree as a whole.

More generally, we may express a dynamic crown rise model dependent on crown coverage (i.e., projected crown area per unit land area) as:

$$\frac{dH_C}{dt} = S(C) \frac{dH}{dt} \quad (44)$$

where  $C$  is crown coverage ( $\text{m}^2 \text{m}^{-2}$ ) and  $S(C) \geq 0$  is a crown-rise function dependent on crown coverage. This general formulation allows for a continuous (Mäkelä 1997) as well as a stepwise (Valentine et al. 1992) crown height function. This formulation also easily relates to several empirical models of crown height, often defined as:

$$H_C = \begin{cases} 0, & \text{if } H < H_m; \\ f(H, \text{competition}), & \text{if } H > H_m \end{cases} \quad (45)$$

A simple case with  $S(C) = 0$  until an age when crown coverage reaches the limiting value,  $H_m$ , and  $S(C) = 0.7$  afterwards, is illustrated in Figure 6.

#### NPP and NEE

Net primary productivity (NPP) is the rate of net production per unit land area ( $\text{kg C ha}^{-1} \text{year}^{-1}$ ). This is equivalent to gross primary productivity (i.e., the rate of photosynthesis per unit land area) less the rate of autotrophic respiration per unit land area. Under our assumptions, total net production in a tree ( $P_{\text{net}}$ ) from year  $t_1$  to year  $t_2$  is approximately:

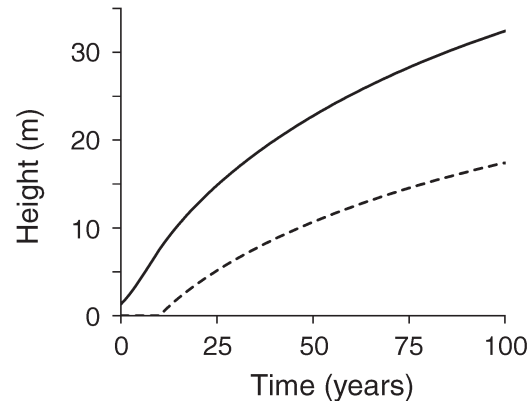


Figure 6. Simulation of tree height (solid line) and crown height (dashed line), applying the empirical crown rise model of Equation 45 in Equation 44 with  $S(C) = 0$  if  $H_C < 7$  m and  $S(C) = 0.7$  if  $H_C > 7$  m.

$$\begin{aligned} P_{\text{net}} \doteq & (\rho_F + \rho_R)(A_{t_2}^+(h) - A_{t_1}^+(h)) \\ & + \left( \frac{\rho_F}{v_F} + \frac{\rho_R}{v_R} \right) (A_{t_1}^+(h) - A_{t_2}^-(h)) \\ & + \rho_W(\beta_1 H_{t_2} + \beta_2 H_{C,t_2})(A_{t_2}^+(h) - A_{t_1}^+(h)) \\ & + \rho_W \beta_1 (H_{t_2} - H_{t_1})(A_{t_1}^+(h) - A_{t_2}^-(h)) \end{aligned} \quad (46)$$

where  $v_F$  and  $v_R$ , respectively, are leaf and feeder root longevity (years). The formula is constructed from the difference equations; it is not the exact integral of Equation 34. The four lines of the formula, respectively, account for (i) biomass of new leaves and feeder roots that attach to new sapwood pipes, (ii) biomass of new leaves and feeder roots that attach to old elongating pipes, (iii) biomass of new sapwood due to secondary growth, and (iv) biomass of new sapwood due to elongation. In a pure stand, which comprises  $N$  trees and occupies land area  $|A|$  (ha), NPP is approximately:

$$\text{NPP} \doteq \frac{1}{|A|} \sum_k^N \frac{P_{\text{net}k}}{t_2 - t_1} \quad (47)$$

Net ecosystem productivity (NEP) is NPP less the rate of heterotrophic respiration per unit land area ( $\text{kg C ha}^{-1} \text{year}^{-1}$ ). Net ecosystem exchange (NEE) is equivalent to NEP plus the flux of dissolved organic carbon, i.e., the rate at which carbon enters or leaves in moving water. To put it another way, NEE is the rate of change in the carbon stock per unit land area. In a pure stand, the carbon tied up in live trees can be approximated with the biomass Equations 8, 9, 16 and 31. However, these equations do not account for the relatively small amounts of carbon in unpruned dead branches and bark.

#### Discussion

Equations 26, 27, 38 and one of the crown rise options suffice to grow a model stand comprising individual model trees. Alternatively, Equation 28 may substitute for Equations 26 and 27. Each year, new crown height is calculated first, followed by new tree height, and then sapwood area or basal area or



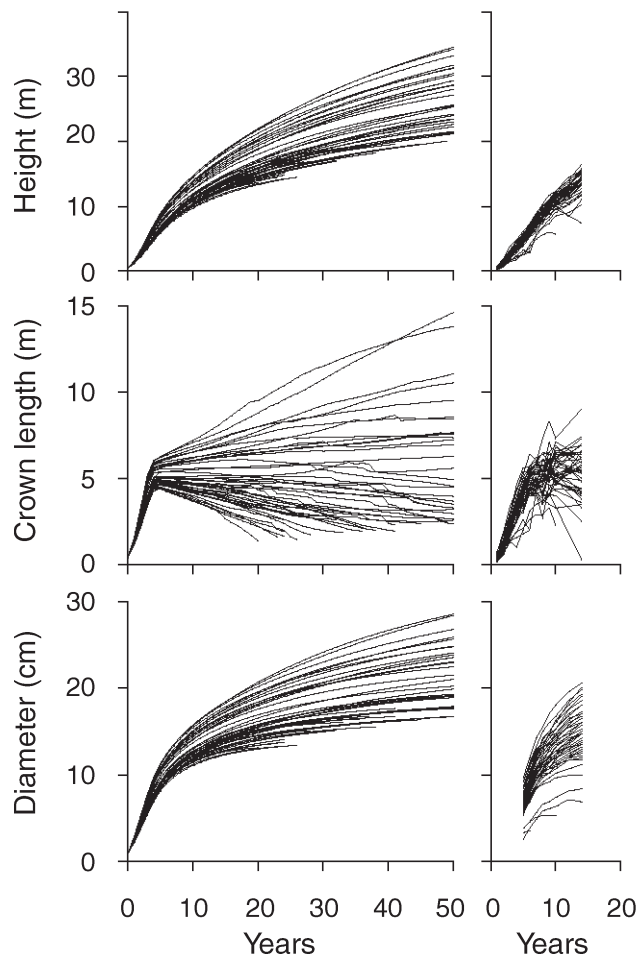


Figure 7. Left: simulation of a growth plot with 49 loblolly pine (*Pinus taeda*) trees. Self-thinning begins in Year 18. Right: measured trajectories. See Appendix for details.

both. In most of our work with these equations, we have assumed that a tree dies when its live crown ratio shrinks to less than 10%. Differentiation in the growth rates of model trees can be induced by a small random effect added or subtracted to the specific rate of photosynthesis of each model tree (Figure 7).

We have defined the rate of photosynthesis per unit leaf mass rather than per unit leaf area because the former is reportedly more uniform within a crown (Niinemets and Tenhunen 1997). Some recent studies even suggest that structural acclimation is sufficient to make the annual mean photosynthetic rate per unit foliage mass almost independent of crown position in the canopy (Stenberg et al. 2001, Vanninen 2003). We have not specified an explicit effect of foliar density (i.e., leaf mass per unit land area) on the rate of photosynthesis, though there is an indirect connection: some decrease in the specific rate of photosynthesis occurs with increasing tree height in concert with the hydraulic limitation hypothesis, i.e., Equation 33. Before closure, tree height is equivalent to crown length, which is effectively related to leaf mass by Equation 19. Mäkelä (1997) accounted for hydraulic limitation by specifying a decrease in the specific rate of photosynthesis with increasing crown length (see Appendix). This approach

has a similar effect on the rate of photosynthesis.

Pipe model theory and the optimal control model have provided a simple, and perhaps minimal, model for translating physiological rates and morphological ratios into growth rates of inventory variables. From the point of view of carbon balance, this translation is essentially about rules of carbon allocation, while assuming that the total annual carbon gain can be estimated. The long-term growth pattern is more sensitive to carbon allocation than to year-to-year variation of specific metabolic rates. Constraining the allocation by observed structural relationships together with the carbon balance makes the model robust yet reasonably flexible to account for the wide variation of individual growth rates encountered in forest stands (Figure 7). Many other carbon balance models focus on estimating photosynthesis and respiration from weather and available resources, such as soil nitrogen and water, at shorter time steps. Integration of these low-level process models for estimating the mean annual physiological rates used in the present model should provide a fruitful link between effects of weather, site and inherent growth pattern.

Whether the present model will be accepted by the forest modeling community cannot be predicted. But it seems a logical step in the evolution of a process-based model for practical use in forecasting forest growth. We recognize that our theory and knowledge has not yet advanced to the point where it might afford the formulation of a “standard model” that everyone would be happy with, and perhaps it never will. Assumptions and trade-offs between practicality and detail must be made in the course of a formulation of any forecasting model. However, any forest model, standard or otherwise, need not be chiseled in stone; rather it should be subjected to unremitting scrutiny so that it may evolve as we improve our theory and knowledge. If the forest modeling community were to pursue an evolving standard model, we could estimate or measure the same parameters and learn from the resultant differences within and among species and environments.

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## Appendix

### Estimation of $z$ with a stem taper model

Our objective is an estimate of  $z$  for Equation 19 and the functions that derive from it. We generalize Equation 19 to apply at any point on the main stem within the crown:

$$A^*(l) = \beta_3 l^z \quad 0 < l \leq L_C \quad (\text{A1})$$

where  $A^*(l)$  is cross-sectional area of the main stem at a distance  $l$  (m) from the tip. In theory (West et al. 1999),  $z$  is constant over the length of the crown, so:

$$\frac{A^*(l_2)}{A^*(l_1)} = \frac{l_2^z}{l_1^z} \quad (\text{A2})$$

Given two sets of measurements:

$$\hat{z} = \frac{\log A^*(l_2) - \log A^*(l_1)}{\log l_2 - \log l_1} \quad (\text{A3})$$

Alternatively, estimating  $A^*(l)$  with a stem taper model at  $l_1 = L_C/2$  and  $l_2 = L_C$ :

$$\frac{\hat{A}^*(L_C)}{\hat{A}^*(L_C/2)} \doteq \left( \frac{L_C}{L_C/2} \right)^z = 2^z \quad (\text{A4})$$

Hence,

$$\hat{z} = \frac{\log \hat{A}^*(L_C) - \log \hat{A}^*(L_C/2)}{\log 2} \quad (\text{A5})$$

*Derivation of the height growth model*

The rate of production of foliage is (e.g., Valentine 1997):

$$\frac{dW_F^+}{dt} = \rho_F \left( \frac{dA^+(h)}{dt} + \frac{A(h)}{v_F} \right) \quad (\text{A6})$$

Analogously, the rate of production of feeder roots is:

$$\frac{dW_R^+}{dt} = \rho_R \left( \frac{dA^+(h)}{dt} + \frac{A(h)}{v_R} \right) \quad (\text{A7})$$

The time derivative of Equation 16 expresses the growth rate of sapwood biomass in terms of the growth rates  $A(h)$  and  $H$ , and the rate of crown rise, i.e.,

$$\begin{aligned} \frac{dW_W}{dt} = & \rho_W (\beta_1 H + \beta_2 H_C) \left( \frac{dA^+(h)}{dt} - \frac{dA^-(h)}{dt} \right) \\ & + \rho_W A(h) \left( \beta_1 \frac{dH}{dt} + \beta_2 \frac{dH_C}{dt} \right) \end{aligned} \quad (\text{A8})$$

Setting  $dH_C/dt$  and  $dA^-/dt$  to zero isolates the rate of production:

$$\frac{dW_W^+}{dt} = \rho_W (\beta_1 H + \beta_2 H_C) \frac{dA^+(h)}{dt} + \rho_W A(h) \beta_1 \frac{dH}{dt} \quad (\text{A9})$$

Substituting Equations 8, 9, 16, 23 and A6, A7 and A9 into Equation 34 and solving for the growth rate of tree height:

$$\frac{dH}{dt} = g_1 (H - H_C) \left( \frac{g_2 - (g_4 - 1)H_C - H}{g_3 + (g_5 - 1)H_C + H} \right) \quad (\text{A10})$$

where:

$$g_0 = \rho_F s_1 + \rho_W m_W \beta_1 \quad (\text{A11})$$

$$g_1 = \frac{1}{1+z} \left( \frac{g_0}{\beta_1 \rho_W (1+c)} \right) \quad (\text{A12})$$

$$g_2 = \left( \frac{\rho_F (s_0 - m_F) - \rho_R m_R}{g_0} \right) - \frac{(1+c)}{g_0} \left( \frac{\rho_F}{v_F} + \frac{\rho_R}{v_R} \right) \quad (\text{A13})$$

$$g_3 = \frac{z}{1+z} \left( \frac{\rho_F + \rho_R}{\rho_W \beta_1} \right) \quad (\text{A14})$$

$$g_4 = 1 + \left( \frac{\rho_W m_W \beta_2}{g_0} \right) \quad (\text{A15})$$

$$g_5 = \frac{z}{1+z} \left( \frac{\beta_1 + \beta_2}{\beta_1} \right) = \frac{z}{1+z} \left( \frac{1}{\beta_B + \beta_S} \right) \quad (\text{A16})$$

Mäkelä (1997) used an alternative to Equation 33 to model the effect of hydraulic limitation, in effect substituting crown length for tree height. In the present notation:

$$s = s_0 - s_1 L_C = s_0 - s_1 H + s_1 H_C \quad (\text{A17})$$

which yields:

$$g_4 = 1 + \left( \frac{\rho_W m_W \beta_2 - \rho_F s_1}{g_0} \right) \quad (\text{A18})$$

*Details of Figure 7*

The projections shown in Figure 7 were generated with the following parameter values:  $c = 0.25$ ,  $m_F = 0.7$ ,  $m_R = 0.35$ ,  $m_W = 0.075$ ,  $s_1 = 0.075$ ,  $z = 1.7$ ,  $\alpha = 15.5^\circ$ ,  $\beta_B = 0.47$ ,  $\beta_R = 0.5$ ,  $\beta_S = 0.3$ ,  $v_F = 2$ ,  $v_R = 0.5$ ,  $\rho_F = 270$ ,  $\rho_R = 88$  and  $\rho_W = 220$ . Similar results can be achieved with other parameter values (Mäkelä and Valentine 2001).

The mean specific rate of photosynthesis was fixed at  $s_0 = 7.5$ . Variation among model trees was achieved with  $s_0 \pm u s_0$ , where  $u$  was uniform random deviate drawn from  $U[0,0.1]$ . Crown rise was calculated in 16 directions for each model tree and then averaged (see Valentine et al. 2000). Death of a model tree was assumed when its live crown ratio shrank to 0.15. The real-tree data come from a loblolly pine spacing trial on the Piedmont Plateau of Virginia (Amateis et al. 1988). Planted trees were spaced 2.44 m apart on a square grid. Initial tree diameters averaged 1.1 cm and heights averaged 0.5 m.