Height Growth, Site Index, and Carbon Metabolism

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A metabolic model of height growth and site index is derived from a parametrization of the annual carbon balance of a tree. The parametrization is based on pipe-model theory. Four principal variants of the height-growth model correspond to four combinations of assumptions regarding carbon allocation: (a) the apical shoot is autonomous or (b) it is not; and (A) the specific rate of elongation of a shoot equals that of a woody root or (B) it does not. The bB model is the most general as it includes the aA, bA, and aB models as special cases. If the physiological parameters are constant, then the aA model reduces to the form of the Mitscherlich model and the bA model to the form of a Bertalanffy model. Responses of height growth to year-to-year variation in atmospheric conditions are rendered through adjustments of a subset of the model's parameters, namely, the specific rate of production of carbon substrate and three specific rates of maintenance respiration. As an example, the effect of the increasing atmospheric concentration of CO_2 on the time-course of tree height of loblolly pine is projected over 50-year span from 1986. Site index is predicted to increase and, more importantly, the shape of the site-index curve is predicted to change.

Keywords Bertalanffy model, carbon allocation, carbon balance, carbon dioxide, Mitscherlich model, pipe-model theory

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1 Introduction

Empirical forest-growth models have been constructed for a great number of species and locations. Of those models which pertain to even-aged stands, many use site index (I) – the average height of dominant trees (H) at a specified stand age – as the principal scaling parameter. The value of I determines the time-course of H and, to some degree, the time-courses of variables related to H such as average basal area, volume, and dry matter.

The *site* in site index seems to connote perma-

nence in the sense that the value of I for a given species and location is expected to remain constant with the elapse of time. Yet the environments of all forest stands are indisputably changing due to the increasing concentration of CO_2 in the atmosphere. The current rate of increase is about 1.6 ppm per year (Conway et al. 1991) and this rate is expected to increase in the next few decades. Thus, site indices most everywhere probably will change to some degree rendering yield tables and empirical forest-growth models inaccurate. To understand how this global change may affect site index, we first need to understand how height growth varies with rates of metabolism and allocation of carbon in forest trees.

Several telionomic/mechanistic models have been advanced that define the rate of woody production in terms of rates of metabolism and allocation of carbon (see, e.g., reviews by Dixon et al. (1990) and Cannell and Dewar (1994)). Models derived by Valentine (1988, 1990) partition the carbon used in woody production according to whether the production lengthens stems and woody roots or thickens them. In an anatomical sense, this method differentiates the woody production which derives from the cellular division of shoot/root meristems from that which derives from lateral meristems. The rate of lengthening of shoots and woody roots is described by a differential equation that converts to models of height growth under reasonable assumptions. Consequently, it is possible to model height growth as a function of rates of metabolism and allocation of carbon and to discern – insofar as the metabolic model is correct – how site index may be altered by changes in these rates. The purpose of this paper is to interpret and discuss height growth and site index in light of the metabolic model. We begin with a brief excursus on site-index curves.

1.1 Site Index

Site index, I, usually is defined as the value of H at stand age 25 or 50 years, though any desired stand age could substitute. Many equations have been used to model the time-course of H, including the Mitscherlich equation (e.g., Carmean 1972; West 1993) and the Bertalanffy equation (e.g., Trousdell et al. 1974; Newberry and Pienaar 1978; Garcia 1983; Deleuze and Houllier 1995). We shall briefly focus on the Mitscherlich and Bertalanffy equations because the metabolic model reduces to these forms under reasonable assumptions.

The Bertalanffy equation describes the growth rate of H with three parameters (α, β, and c):

$$dH / dt = (\alpha / c)H^{1-c} - (\beta / c)H \qquad (1a)$$

where t is time (yr). This equation can be multiplied by cH^{c-1} to put it in a form that allows an initial value at time t_0 of $H(t_0) = 0$:

$$dH^c / dt = \alpha - \beta H^c . \qquad (1b)$$

The parameters usually take values such that $\alpha >> \beta > 0$ and $1 \geq c > 0$. The Mitscherlich equation, $dH/dt = \alpha - \beta H$, results if $c = 1$. The time-course of H obtains from the solution of eqn (1), *viz.*,

$$H(t) = \left\{ \frac{\alpha}{\beta} - \left[\frac{\alpha}{\beta} - H^c(t_0) \right] \exp[-\beta \cdot (t - t_0)] \right\}^{1/c} \qquad (2)$$

$$t \geq t_0 .$$

Assuming a stand reaches its "index age" in year t_I, then $I = H(t_I)$, i.e.,

$$I = \left\{ \frac{\alpha}{\beta} - \left[\frac{\alpha}{\beta} - H^c(t_0) \right] \exp[-\beta \cdot (t_I - t_0)] \right\}^{1/c} . \qquad (3)$$

Once I is ascertained, the time-course of H can serve as a "guide curve" for the calculation of proportional or anamorphic site-index curves. For example, if I_1 and I_2, respectively, are the site indices of two anamorphic time-courses, $H_1(t)$ and $H_2(t)$, then

$$H_2(t) = (I_2 / I_1) \cdot H_1(t) \quad t \geq t_0 . \qquad (4)$$

Non-proportional or polymorphic sets of site-index curves also are used. In a polymorphic set, the values of the parameters α, β, and c would be specified as functions of I (see, e.g., Trousdell et al. 1974; Clutter et al. 1983; Furnival et al. 1990).

2 The Metabolic Model

2.1 Elongation

As was noted, theory underlying a metabolic model of tree growth was detailed by Valentine (1990). In this section we use those aspects of the theory which pertain to height growth.

For modeling purposes, a tree is differentiated into foliar (F), feeder-root (R), and woody (W) dry matter (kg C). The rates of production of these components are denoted dF^+/dt, dR^+/dt, and dW^+/dt, respectively, where time, t, is measured in years. The sum of these rates of production plus the rates of coincident constructive respiration are formulated as a carbon balance:

$$\begin{aligned}&(1+c_F)\mathrm{d}F^+/\mathrm{d}t+(1+c_R)\mathrm{d}R^+/\mathrm{d}t\\&+(1+c_W)\mathrm{d}W^+/\mathrm{d}t=\bar{s}F\\&-(\bar{m}_F F+\bar{m}_R R+\bar{m}_W W^*)\end{aligned}\qquad(5)$$

where c_i ($i = F,R,W$) is the number of units of C substrate consumed in constructive respiration to the produce a unit of dry matter (kg C (kg C)$^{-1}$); $\bar{s}$ is the specific rate of production of C substrate, i.e., the number of units of C substrate produced per unit foliar dry matter per unit time (kg C (kg C)$^{-1}$ yr^{-1}); and $\bar{m}_i$ ($i = F,R,W$) is the specific rate of maintenance respiration, i.e., the units of C substrate consumed to maintain a unit of live dry matter per unit time (kg C (kg C)$^{-1}$ yr^{-1}). W^* is the live, respiring portion of W, i.e., the branches, the live portion of the bole, and the transport roots.

Valentine (1990) used pipe-model theory (Shinozaki et al. 1964 a, b) to parametrize F, R, and W^* and their rates of production in terms of two morphological variables: A, the cross-sectional area (m^2) of the bole of the tree at the base of its crown (also known as the active-pipe area), and $\bar{L}$, the average length (m) of stems plus transport roots (also known as active-pipe length). $\bar{L}$ can be considered the average distance, as the sap flows, from a feeder-root to a leaf. The components of live dry matter expressed in terms of A and $\bar{L}$ are:

$$\begin{aligned}F&=z_F A\\R&=z_R A\\W^*&=z_W A\cdot\bar{L}\end{aligned}\qquad(6)$$

where z_F and z_R, respectively, are foliar and feeder-root dry matter per unit of active-pipe area (kg C m^{-2}) and z_W is woody dry matter per unit wet volume (kg C m^{-3}). The rates of production are:

$$\begin{aligned}\mathrm{d}F^+/\mathrm{d}t&=z_F\,\mathrm{d}A^+/\mathrm{d}t+z_F A/\upsilon_F\\\mathrm{d}R^+/\mathrm{d}t&=z_R\,\mathrm{d}A^+/\mathrm{d}t+z_R A/\upsilon_R\\\mathrm{d}W^+/\mathrm{d}t&=z_W\left(\bar{L}\cdot\mathrm{d}A^+/\mathrm{d}t+A\cdot\mathrm{d}\bar{L}_M/\mathrm{d}t\right)\end{aligned}\qquad(7)$$

where υ_F and υ_R, respectively, are foliar and feeder-root longevity (yr); $z_F A/\upsilon_F (= F/\upsilon_F)$ and $z_R A/\upsilon_R (= R/\upsilon_R)$, respectively, are the rates of replacement of senescent foliar and feeder-root dry matter; and $d\bar{L}_M/dt$ is the rate of elongation of $\bar{L}$ directly due to metabolic processes. Because $\bar{L}$ is an average, its rate of change also is affected by the rates of production and loss of branches and roots of nonaverage length (see Valentine 1990). Finally, dW^+/dt is the rate of production of both W and W^*.

Substituting the right-hand sides of eqns (6) and (7) into eqn (5) yields:

$$\begin{aligned}&\left[z_F(1+c_F)+z_R(1+c_R)+z_W(1+c_W)\bar{L}\right]\mathrm{d}A^+/\mathrm{d}t\\&+A\cdot[z_W(1+c_W)]\mathrm{d}\bar{L}_M/\mathrm{d}t\\&+A\cdot\{[z_F(1+c_F)/\upsilon_F]+[z_R(1+c_R)/\upsilon_R]\}\\&=A\cdot\left(z_F(\bar{s}-\bar{m}_F)-\bar{m}_R z_R-\bar{m}_W z_W\bar{L}\right).\end{aligned}\qquad(8)$$

C substrate is allocated to the replacement plus coincident constructive respiration of foliar and feeder-root dry matter at rate $A\cdot\{[z_F(1+c_F)/\upsilon_F]+[z_R(1+c_R)/\upsilon_R]\}$. Subtracting this quantity from both sides of eqn (8) we obtain the rate at which C substrate is allocated to all other production plus constructive respiration:

$$\begin{aligned}&\left[z_F(1+c_F)+z_R(1+c_R)+z_W(1+c_W)\bar{L}\right]\mathrm{d}A^+/\mathrm{d}t\\&+[z_W(1+c_W)]A\cdot\mathrm{d}\bar{L}_M/\mathrm{d}t\\&=A\cdot\{z_F(\bar{s}-\bar{m}_F)-\bar{m}_R z_R-\bar{m}_W z_W\bar{L}\\&-[z_F(1+c_F)/\upsilon_F]-[z_R(1+c_R)/\upsilon_R]\}.\end{aligned}\qquad(9)$$

A fraction, $\bar{\eta}$ ($0<\bar{\eta}<1$), of this C substrate is allocated to root/shoot meristems for the elongation plus constructive respiration of stems and transport roots, therefore,

$$A \cdot [z_W(1+c_W)]\mathrm{d}\bar{L}_M / \mathrm{d}t = \bar{\eta} \cdot A \cdot \{z_F(\bar{s} - \bar{m}_F) - \bar{m}_R z_R - \bar{m}_W z_W \bar{L} - [z_F(1+c_F)/\upsilon_F] - [z_R(1+c_R)/\upsilon_R]\}. \quad (10)$$

Solving for $\mathrm{d}\bar{L}_M / \mathrm{d}t$, we obtain:

$$\mathrm{d}\bar{L}_M / \mathrm{d}t = \bar{a} - b\bar{L} \quad (11)$$

where,

$$\bar{a} = \frac{\bar{\eta}}{z_W(1+c_W)} \cdot \left[z_F(\bar{s} - \bar{m}_F) - z_R\bar{m}_R - \frac{z_F(1+c_F)}{\upsilon_F} - \frac{z_R(1+c_R)}{\upsilon_R} \right] \quad (12)$$

$$b = \frac{\bar{\eta}\,\bar{m}_W}{1+c_W}.$$

The values of the constructive respiration parameters often are assumed equivalent (i.e., $c_F = c_R = c_W$). Under this assumption,

$$\bar{a} = \frac{\bar{\eta}}{z_W} \left[\frac{z_F(\bar{s} - \bar{m}_F) - z_R\bar{m}_R}{1+c_W} - \frac{z_F}{\upsilon_F} - \frac{z_R}{\upsilon_R} \right]. \quad (13)$$

2.2 Height Growth

As was noted, $\mathrm{d}\bar{L}_M / \mathrm{d}t$ is the rate of elongation – due to C metabolism and allocation – of the average length of woody structure between a feeder root and a leaf. Our current interest, however, is not with this particular quantity, but with H, the height of a dominant tree. To derive an equation for $\mathrm{d}H/\mathrm{d}t$ we focus on the individual shoots in a crown. In accordance with pipe-model theory, we assume that the ith shoot is the distal end of an active pipe with cross-sectional area A_i that connects $z_F A_i$ units of foliar dry matter to $z_R A_i$ units of feeder-root dry matter. We assume that the cross-sectional area of each active pipe is constant over it's length and, in the years following it's production, constant over time. The aggregate cross-sectional area of the active pipes, A, changes as new pipes are produced and old pipes are lost to supression and crown rise.

Let L_i denote the length of the ith active pipe, where $\sum_i (A_i / A) \cdot L_i = \bar{L}$.

Substituting for $\bar{L}$ in eqn (11), we obtain:

$$\sum_i (A_i / A) \cdot \mathrm{d}L_i / \mathrm{d}t = \sum_i (A_i / A) \cdot (\bar{a} - bL_i)$$

or,

$$\sum_i A_i \cdot \mathrm{d}L_i / \mathrm{d}t = \sum_i A_i \cdot (\bar{a} - bL_i) \quad (14)$$

Like eqn (11), eqn (14) pertains to elongation of all shoots and roots collectively. We shall derive rates of elongation for individual pipes under two contrasting assumptions: (1) pipes are metabolically autonomous with respect to elongation or (2) they are not.

2.2.1 Autonomous pipes

Under our "pipe-model" assumptions, shoot elongation from a bud is synonymous to the elongation of the aboveground portion of an active pipe. For autonomous elongation, we assume that the foliage attached to the ith pipe produces all of the C substrate for that pipe's elongation. Thus, different rates of elongation may obtain from different specific rates of production of C substrate.

We let s_i denote the specific rate of production of C substrate by the foliage attached to the ith pipe, where $\sum_i (A_i / A) \cdot s_i = \bar{s}$.

Substituting s_i for $\bar{s}$ in eqn (13) provides a_i instead of $\bar{a}$, i.e.,

$$a_i = \frac{\bar{\eta}}{z_W} \left[\frac{z_F(s_i - \bar{m}_F) - z_R\bar{m}_R}{1+c_W} - \frac{z_F}{\upsilon_F} - \frac{z_R}{\upsilon_R} \right]. \quad (15)$$

Because $\sum_i (A_i / A) \cdot a_i = \bar{a}$,

we can replace $\bar{a}$ with a_i in eqn (14), whence

$$\sum_i A_i \cdot \mathrm{d}L_i / \mathrm{d}t = \sum_i A_i \cdot (a_i - bL_i). \quad (16)$$

Let $i = H$ index the apical shoot and pipe. From eqn (16) we extract:

$$A_H \cdot \mathrm{d}L_H / \mathrm{d}t = A_H \cdot (a_H - bL_H). \quad (17)$$

If $\mathrm{d}H / \mathrm{d}t = \gamma \mathrm{d}L_H / \mathrm{d}t$, where γ is the aboveground fraction of elongation, then the growth rate of height is:

$$\mathrm{d}H / \mathrm{d}t = a_H \gamma - bH. \quad (18)$$

If γ, a_H, and b are constant over time, then eqn (18) has the form a Mitscherlich equation. A sigmoidal time-course for H may arise if (*i*) the specific rate of production of C substrate initially increases from year to year and then levels off, or (*ii*) the aboveground fraction of elongation increases (and, therefore, the ratio of stem to root length increases) as the tree grows. For example, we obtain an increasing stem to root ratio if we assume an allometric relation between $H(t)$ and $L_H(t)$ (i.e., $dH^c/dt = \gamma^* dL_H/dt$, where $0 < c \leq 1$ and $\gamma^* = H^c(t)/L_H(t)$ for $t_0 \leq t$). Substituting this relation into eqn (17), we find that the resultant height-growth model has the form of a Bertalanffy equation, i.e.,

$$dH^c / dt = a_H \gamma^* - bH^c . \tag{19}$$

Autonomous pipes also may manifest different rates of elongation because a different fraction of C substrate is allocated to elongation in each pipe. Let η_i denote the fraction of available C substrate allocated to elongation of the *i*th pipe. The rate of elongation is:

$$dL_i / dt = (\eta_i / \overline{\eta}) \cdot (a_i - bL_i) = a_i^* - b_i^* L_i$$

and the growth rate of height is:

$$dH / dt = (a_H^* \gamma - b_H^* H) . \tag{20}$$

Allocation fractions that vary across pipes are inconsistent with the "whole-tree" model, as presented above, unless

$$\sum_i (A_i / A) \cdot (a_i^* - b_i^* L_i) = \overline{a} - b\overline{L} .$$

2.2.2 *Non-autonomous pipes*

^{14}C tracing studies (see, e.g., a review by Sprugel et al. 1991) have demonstrated that for some species, imported C substrate may contribute to the elongation of shoots, particularly apical shoots. The pool of C substrate for production and respiration naturally increases with the total foliar dry matter of the crown. The direction and rate of translocation of C substrate (and other substrates) is thought to depend upon gradients from sources to sinks; Thornley (1972, 1995) has developed mechanistic allocation models based on this premise. For the present model we assume that an elongating non-autonomous apical shoot is a strong sink and, after the seedling year, a net importer of C substrate.

Non-autonomous apical shoots correspond to the distal ends of non-autonomous active pipes in our model. The rate at which aggregate woody volume accrues from elongation of individual pipes is given by eqn (16). Multiplying both sides of that equation by $z_W^* = z_W \cdot (1 + c_W)$ converts it to the rate at which C substrate is allocated for elongation and associated constructive respiration, i.e.,

$$z_W^* \sum_i A_i \cdot dL_i / dt = z_W^* \sum_i A_i \cdot (a_i - bL_i) .$$

We segregate terms pertaining to the apical pipe from those pertaining to other pipes, i.e.,

$$z_W^* \cdot \left[A_H \cdot dL_H / dt + \sum_{i \neq H} A_i \cdot dL_i / dt \right] = z_W^* \cdot \left[A_H \cdot (a_H - bL_H) + \sum_{i \neq H} A_i \cdot (a_i - bL_i) \right] . \tag{21}$$

On the right-hand side is $z_W^* \sum_{i \neq H} A_i \cdot (a_i - bL_i)$, the rate at which C substrate from the non-apical pipes is allocated to elongation and associated constructive respiration. A fraction ($\phi A_H / A$, where $0 \leq \phi < A/A_H$) of this C substrate is allocated or exported to the apical pipe. The elongating, non-autonomous, apical pipe uses its own C substrate at rate $z_W^* A_H \cdot (a_H - bL_H)$ together with imported C substrate at rate

$$(\phi A_H / A) \cdot z_W^* \sum_{i \neq H} A_i \cdot (a_i - bL_i) ;$$

therefore:

$$z_W^* A_H \cdot dL_H / dt = z_W^* \cdot \left[A_H \cdot (a_H - bL_H) + \frac{\phi A_H}{A} \sum_{i \neq H} A_i \cdot (a_i - bL_i) \right] . \tag{22}$$

We note that upon subtraction of eqn (22) from (21), the residual is the rate of allocation of C substrate among the elongating non-apical pipes:

$$z_W^* \sum_{i \neq H} A_i \cdot dL_i / dt = z_W^* \cdot \left(1 - \frac{\phi A_H}{A} \right) \sum_{i \neq H} A_i \cdot (a_i - bL_i) .$$

Of prime interest, however, is eqn (22). Substituting $A \cdot (\bar{a} - b\bar{L}) - A_H \cdot (a_H - bL_H)$ for $\sum_{i \neq H} A_i \cdot (a_i - bL_i)$ and solving for the rate of elongation of the apical pipe, we obtain:

$$dL_H / dt = \left(1 - \frac{\phi A_H}{A}\right)(a_H - bL_H) + \phi \cdot (\bar{a} - b\bar{L}). \quad (23)$$

Eqn (23) has interesting properties. Initially, $A = A_H$ and $\bar{L} = L_H$ and, therefore, $\bar{a} = a_H$ and $dL_H / dt = a_H - bL_H$. When $A >> A_H$ the rate of elongation is $dL_H / dt \doteq a_H - bL_H + \phi \cdot (\bar{a} - b\bar{L})$. If $\bar{L} \to \bar{a} / b$ then $dL_H / dt \to (a_H - bL_H)$. Thus, the asymptotic length of the non-autonomous apical pipe is $L_H(\infty) = a_H / b$, the same as that of an autonomous apical pipe (see eqn 18).

We can remove $\bar{L}$ from the model if we assume that the rate of import of C substrate is

$$\left(\frac{z_W^* \xi A_H}{A}\right)[A \cdot (a_H - bL_H) - A_H \cdot (a_H - bL_H)]$$

instead of

$$\left(\frac{z_W^* \phi A_H}{A}\right)[A \cdot (\bar{a} - b\bar{L}) - A_H \cdot (a_H - bL_H)].$$

The resultant model is:

$$dL_H / dt = \left\{1 + \xi \cdot \left[1 - \frac{A_H}{A}\right]\right\}(a_H - bL_H) \quad (24)$$

where $\xi \geq 0$ is a dimensionless scaling parameter. To remove A from this model we use eqns (9) and (10) from which we obtain:

$$(1 / A) dA^+ / dt = [\lambda / (z + \bar{L})] d\bar{L}_M / dt.$$

where $\lambda = (1 - \overline{\eta}) / \overline{\eta}$ and $z = (z_F + z_R) / z_W$. Prior to crown rise $d\bar{L}_M / dt = d\bar{L} / dt$ and $dA^+ / dt = dA / dt$, therefore,

$$(1 / A) dA / dt = [\lambda / (z + \bar{L})] d\bar{L} / dt$$

Upon integration, we find that

$$A \propto (z + \bar{L})^{\lambda}$$

and, therefore, when it matters (i.e., when the tree is small),

$$\frac{A_H}{A} = \left(\frac{z + \bar{L}(t_0)}{z + \bar{L}}\right)^{\lambda} \doteq \left(\frac{z + L_H(t_0)}{z + L_H}\right)^{\lambda}. \quad (25)$$

Substituting the right-hand side of eqn (25) into (24), and assuming $L_H(t_0) = 0$, we obtain:

$$dL_H / dt = \left\{1 + \xi \cdot \left[1 - \left(\frac{z}{z + L_H}\right)^{\lambda}\right]\right\}(a_H - bL_H). \quad (26)$$

This model displays the same basic behavior as eqn (23) and has an identical intitial growth rate and asymptote.

The substitution of H/γ for L_H in eqn (26) provides the rate of growth of tree height:

$$dH / dt = \left\{1 + \xi \cdot \left[1 - \left(\frac{z\gamma}{z\gamma + H}\right)^{\lambda}\right]\right\}(a_H \gamma - bH). \quad (27)$$

The initial rate of growth is $dH/dt = a_H\gamma$ if $H(0) = 0$ and the asymptote of the solution is $H(\infty) = a_H\gamma/b$. The import of substrate, signified by $\xi > 0$, may yield a sigmoidal time-course for H.

Further elaboration of the model is possible. For example, if we assume, as we did above, that the aboveground fraction of elongation increases with tree height (i.e., $dH^c/dt = \gamma^* dL_H/dt$ where $0 < c \leq 1$ and $\gamma = H^c(t)/L_H(t)$ for $t_0 \leq t$), then

$$dH^c / dt = \left\{1 + \xi \cdot \left[1 - \left(\frac{z\gamma^*}{z\gamma^* + H^c}\right)^{\lambda}\right]\right\}(a_H \gamma^* - bH^c). \quad (28)$$

Finally, we should note that the difference $s_H - \overline{m}_F$, is used to calculate a_H (see eqn 15). This difference is the annual specific rate of assimilation of unshaded foliage, a quantity that can be estimated in the field.

3 Solutions

Estimated values of the parameters of the metabolic model for loblolly pine (*Pinus taeda* L.) in Buckingham County, Virginia, are listed in Table 1. Solutions of eqns (18) and (27) are depicted in Fig. 1a. The points in the figure are average heights of the 7 tallest of 49 trees in a 1.83 m × 1.83 m spacing plot. Early height growth under the assumption of import of carbon (eqn 27) naturally exceeds that under the assumption of

Table 1. Parameters of the metabolic model.

Symbol	Definition	Value*	Units
c_F	Respiratory cost of production of foliage	0.25	kg C (kg C)$^{-1}$
c_R	Respiratory cost of production of feeder roots	0.25	kg C (kg C)$^{-1}$
c_W	Respiratory cost of production of woody tissues	0.25	kg C (kg C)$^{-1}$
$\overline{m}_F$	Specific rate of maintenance respiration of foliage	0.70	kg C yr^{-1} (kg C)$^{-1}$
$\overline{m}_R$	Specific rate of maintenance respiration of feeder roots	0.35	kg C yr^{-1} (kg C)$^{-1}$
$\overline{m}_W$	Specific rate of maintenance respiration of live woody tissues	0.166	kg C yr^{-1} (kg C)$^{-1}$
s_H	Specific rate of production of carbon substrate of unshaded foliage	9.0	kg C yr^{-1} (kg C)$^{-1}$
z_F	Foliar dry matter per unit cross-sectional area of bole at the base of the live crown	270	kg C m^{-2}
z_R	Feeder-root dry matter per unit cross-sectional area of bole at the base of the live crown	88	kg C m^{-2}
z_W	Woody dry matter per unit wet volume	220	kg C m^{-3}
γ	Aboveground fraction of tree length	0.67	m^3 m^{-3}
γ_1	Aboveground fraction of tree length at age 1	0.50	m^3 m^{-3}
γ_∞	Aboveground fraction of tree length at old age	0.75	m^3 m^{-3}
$\overline{\eta}$	Fraction of the carbon substrate pool allocated to elongation of shoots and roots	0.28	kg C (kg C)$^{-1}$
ξ	Carbon import parameter	0.15	–
υ_F	Longevity of foliage	2	yr
υ_R	Longevity of feeder roots	0.5	yr

*Estimates for loblolly pine in Buckingham County, Virginia.

carbon autonomy (eqn 18). After early divergence, the time-courses of tree height under the two assumptions converge toward a common asymptote, as they must.

The solution of eqn (19) is compared to that of its non-autonomous variant (eqn 28) in Fig. 1b. The value of c is:

$$c = \frac{\ln[L_H(\infty)] - \ln[L_H(1)]}{\ln[H(\infty)] - \ln[H(1)]}.$$

Let $\gamma_1 = H(1)/L_H(1)$ and $\gamma_\infty = H(\infty)/L_H(\infty) = H(\infty)/(a_H/b)$, then

$$c = \frac{\ln[a_H / b] - \ln[H(1)/\gamma_1]}{\ln[\gamma_\infty a_H / b] - \ln[H(1)]}.$$

For the time-courses in Fig. 1b, $H(1) = 0.42$ m, $\gamma_1 = 0.5$, $\gamma_\infty = 0.75$; therefore, $c = 0.9097$ and $\gamma^* = H^c(1)/L_H(1) = 0.5408$. These time-courses, like those in Fig. 1a, converge toward a common asymptote, but the asymptotic height is taller than that of the other two models because $c < 1$. However, the asymptotic apical-pipe length, a_H/b, is the same for all four models.

Most of the parameter values in Table 1 were borrowed from previous studies (Valentine et al. 1997a,b); details regarding the estimation of the parameter values are given in the latter paper. Estimated for the present paper were the values of γ_1, γ_∞, s_H, and ξ. The values of γ_1 and γ_∞ are educated guesses. The specific rate of production of C substrate of unshaded foliage, s_H, and the carbon-import parameter, ξ, were estimated with 12 remeasurements of dominant tree height in a spacing experiment initiated in 1983 (Amateis et al. 1988). The estimation involved integrating the height-growth model, given initial estimates of s_H and ξ, and then calculating the sum of squares of residuals with the height data. New estimates of the parameters were generated by an optimization (i.e., simplex) algorithm and the entire procedure was repeated until the sum of squares of residuals converged to an apparent minimum. Eqn (27) was used in the estimation process.

The two non-autonomous models, given the parameter values in Table 1, show good agreement with actual early height growth (Fig. 1b). The two autonomous models (eqns 18 and 19) would show better agreement with actual early

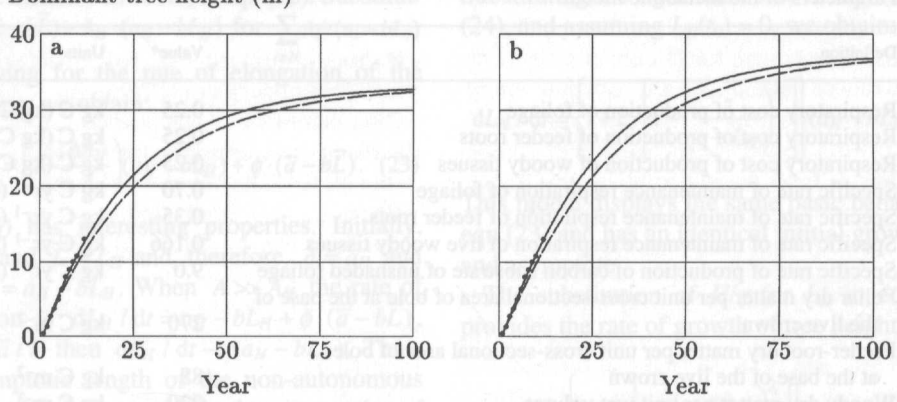

Fig. 1. Solutions of the four principal variants of the height-growth model calculated with the parameter values in Table 1. On the left (a) are solutions of eqn (18), dash; eqn (27), solid. On the right (b) are solutions of eqn (19), dash; eqn (28), solid. The points are measurements from a loblolly pine stand in Buckingham County, Virginia.

height growth if the value of s_H were increased. The degree to which projected site index, $H(25)$, is affected by a 10 % decrease or a 10 % increase in the value of any one of the parameters is depicted in Fig. 2. Site index appears to be most sensitive to changes in the value of s_H.

3.1 Modeling effects of weather and CO_2

As was noted, the concentration of CO_2 in the atmosphere has increased by about 1.6 ppm per year over the last 10 years (e.g., Conway et al. 1991). Assuming a continuation of this rate, we should expect a total increase of 48 to 80 ppm (13 % to 22 %) over the next 30 to 50 years. The question is whether this increase will affect height growth curves and, if so, by how much. Responses of height growth to year-to-year variation in atmospheric conditions, including the concentration of CO_2, can be rendered through annual adjustments of the values of the specific rate of production of C substrate, s_H, and the specific rates of maintenance respiration, $\overline{m}_F$, $\overline{m}_R$, and $\overline{m}_W$.

To explore CO_2-mediated effects on height growth, the carbon-flux model of MAESTRO was used to calculate adjustment factors for s_H. The carbon-flux model has been calibrated for loblolly pine (Jarvis et al. 1990, Horne 1993); it is driven by temperature, photosynthetically active photon flux density, pre-dawn xylem water potential, vapor pressure deficit, and atmospheric CO_2 concentration. Meteorological data for the estimation of the driving variables were obtained for Buckingham County, Virginia, for 1949 to 1992. Streams of the driving variables were estimated on a half-hour timestep for a 50-year span with 1986 through 1992 data followed by 1949 through 1991 data.

The carbon-flux model of MAESTRO provides a steady-state estimate of the specific rate of photosynthesis, $p(\tau)$, where τ is time (s). In the present application, the value of $p(\tau)$ changed each half hour in accord with the timestep of changes in the driving variables. Integration of $p(\tau)$ over the h seconds in year y ($y = 1, 2, ..., 50$) provided an estimate of the annual specific rate of photosynthesis, $P(y)$, i.e.,

$$P(y) = \int_0^h p(\tau)\mathrm{d}\tau .$$

To assess the effect of year-to-year variation in weather, the value of s_H in year y was adjusted to $s_H(y) = s_H P(y) / \overline{P}$, where $\overline{P}$ was the average of the values of $P(y)$ over the 50 years of the projection. To assess the effects of the increasing concentration of CO_2, $\overline{P}$ was calculated with the CO_2 concentration fixed at the 1986 level (344 ppm), then the $P(y)$ were recalculated to include

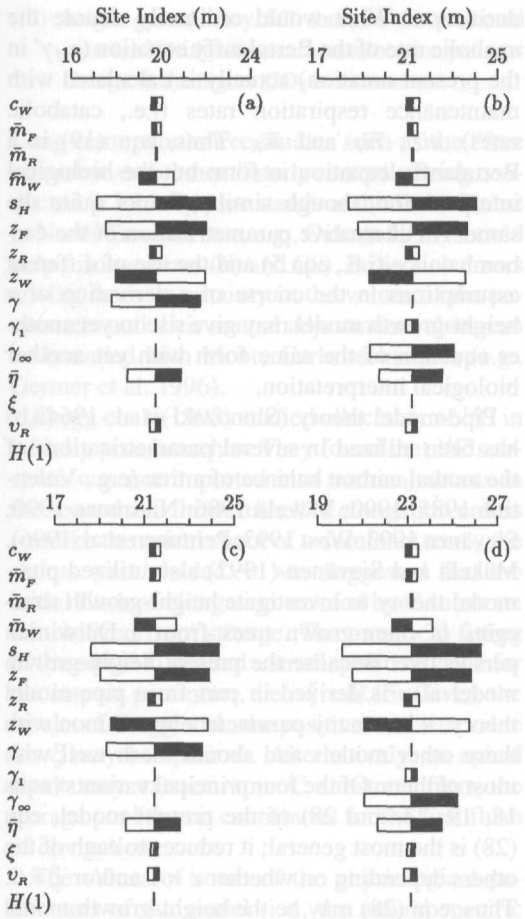

Fig. 2. Change in site index, $H(25)$, induced by a 10 % decrease (open bar) or 10 % increase (solid bar) in the value of the parameter of (a), eqn (18); (b), eqn (19); (c), eqn (27); (d), eqn (28). Default values of the parameters are listed in Table 1. $H(1) = 0.42$ m.

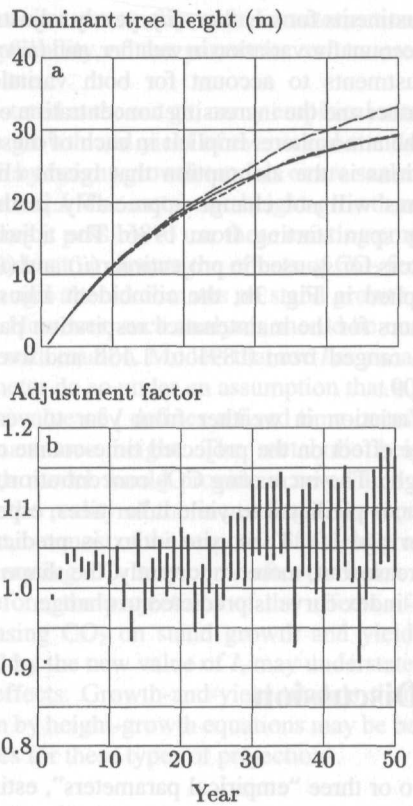

Fig. 3. Above (a) are solutions of eqn (27) calculated with the parameter values in Table 1 with (*i*) no adjustments (solid); (*ii*) yearly adjustments to account for year-to-year variation in weather (short dash); (*iii*) yearly adjustments to account for both weather and the increasing atmospheric concentration of CO_2 (long dash). Below (b) are the adjustment factors of s_H that account for (*i*) year-to-year variation in weather (bottom of bar) and (*ii*) both weather and the increasing atmospheric CO_2 concentration (top of bar).

the effect of the increasing CO_2.

The numerators of adjustment factors, $R(y) / \overline{R}$, for the three specific rates of maintenance respiration, were calculated from the time-course of air temperature, $T(\tau)$:

$$R(y) = \int_0^h Q_{10}^{T(\tau)/10} \, d\tau .$$

Q_{10} generally is defined as the factor by which respiration is assumed to increase, given a 10 °C increase in temperature (e.g., Ryan et al. 1994). $\overline{R}$ is the average of $R(y)$ (y = 1, 2,..., 50). The adjustment factors were calculated with $Q_{10} = 2$; this value falls within the usual range of Q_{10} values (1.9 Q_{10} 2.3, Ryan et al. (1994)) for pines.

Fig. 3a compares projected time-courses of tree height of a loblolly pine – as calculated with the model allowing for import of carbon to the apical meristem (eqn 27) – with (*i*) no yearly

adjustments for weather, (*ii*), yearly adjustments to account for variation in weather, and (*iii*) yearly adjustments to account for both variation in weather and the increasing concentration of CO_2 in the atmosphere. Implicit in each of these projections is the assumption that recent climatic norms will not change appreciably in the 50-year span starting from 1986. The adjustment factors for s_H used in projections (*ii*) and (*iii*) are graphed in Fig. 3b; the coincident adjustment factors for the maintenance respiration parameters ranged from 0.891 to 1.138 and averaged 1.009.

Variation in weather from year to year has little effect on the projected time-course of tree height. The increasing CO_2 concentration, however, is predicted to yield taller trees, especially after age 30. Thus, site index is predicted to increase, but, more importantly, the shape of the site-index curve is predicted to change.

4 Discussion

Two or three "empirical parameters", estimated by least squares or maximium likelihood procedures, usually are sufficient to accurately describe a time-course of the height of a dominant tree. In this paper, we began with a carbon-balance equation of dry-matter production and derived four variants of a metabolic model of height growth, one (eqn 18) which condenses into the form of a two-parameter Mitscherlich equation and another (eqn 19) which condenses into the form of a three-parameter Bertalanffy equation. Bertalanffy (1957) interpreted both the three- and four-parameter versions of his model as equating the growth rate of an organism to the difference between the organism's anabolic and catabolic rates of metabolism. Pienaar and Turnbull (1973) motivated the use of the three-parameter Bertalanffy equation in forestry applications, applying the biological interpretation to individual trees and extending it to even-aged stands.

The three "condensed parameters" ($a_H\gamma^*$, b, and c) of eqn (19) are calculated from combinations of physiological and morphological parameters that were defined in the course of the derivation. What would ordinarily denote the anabolic rate of the Bertalanffy equation ($a_H\gamma^*$ in the present notation) actually is calculated with maintenance respiration rates (i.e., catabolic rates), *viz.*, $\overline{m}_F$ and $\overline{m}_R$. Thus, eqn (19) is a Bertalanffy equation in form but the biological interpretation, though similar, is not quite the same. An alternative parametrization of the carbon balance (i.e., eqn 5) and the use of different assumptions in the course of a derivation of a height-growth model may give rise to yet another equation of the same form with yet another biological interpretation.

Pipe-model theory (Shinozaki et al. 1964a,b) has been utilized in several parametrizations of the annual carbon balance of a tree (e.g., Valentine 1985, 1990; Mäkelä 1986; Nikinmaa 1990; Sievänen 1993; West 1993; Perttunen et al. 1996). Mäkelä and Sievänen (1992) also utilized pipe-model theory to investigate height-growth strategies of open-grown trees from a Darwinian perspective. Because the present height-growth model also is derived in part from pipe-model theory, it has many parameters in common with these other models and should mesh well with most of them. Of the four principal variants (eqns 18, 19, 27, and 28) of the present model, eqn (28) is the most general; it reduces to each of the others depending on whether $c = 1$ and/or $\xi = 0$. Thus, eqn (28) may be the height-growth model of choice for most purposes.

Applied to loblolly pine, the height-growth model predicts a positive effect of the increasing atmospheric concentration of CO_2 in Buckingham County, Virginia, and elsewhere. However, there are good reasons why such predictions should be viewed with skepticism. For example:

(*i*) the climate in the next 30 to 50 years may deviate from the recent norms; increased respiration caused by climatic warming could offset some of the production that otherwise would accrue from increasing CO_2 concentrations (Valentine et al. 1997a).

(*ii*) although recent evidence suggests otherwise (e.g., Ellsworth et al. 1995; Liu and Teskey 1995), loblolly pine may fail to respond positively to the higher CO_2 concentrations; substrates other than carbon (e.g., nitrogen) may limit or become limiting to production in some stands.

(*iii*) height growth may fall short of the predicted increase if within-tree carbon-allocation patterns change in the higher CO_2 environment.

Long-term, whole-tree studies such as the "free air carbon enrichment" study currently being conducted in loblolly pine stands at the Duke Forest in North Carolina (see, e.g., Culotta 1995) should help resolve items (*ii*) and (*iii*). Projection errors arising from uncertainty in the values of the parameters and their annual adjustment values can be bounded with Monte Carlo techniques (e.g., Gertner et al. 1996).

Cregg et al. (1993) studied allocation of ^{14}C in loblolly pine branches. They found that ^{14}C substrate was not imported into terminal shoots in the second and third flushes of elongation unless – unlike the apical shoot of a dominant tree – the shoots were shaded. It was suggested that the initial flush of elongation was fed by C substrate remobilized from storage. The empirical fitting of the eqn (27) yielded a small, positive value for the import parameter, i.e., $\xi = 0.15$. Given the results of Cregg et al., the positive, nonzero value for ξ may be spurious. Alternatively, an apical shoot may extract more C substrate from the storage pool than it contributes for the first flush of elongation.

The values of some of the physiological parameters of the model (i.e., the annual specific rates of substrate production and maintenance respiration) are supposed to vary among locations with latitude, climate, and soil properties. As these physiological rates vary, so too will our estimates of site index. The constructive respiration parameters (i.e., c_F, c_R, and c_W) may be regarded as stoichiometric and, therefore, their values may be regarded as fixed. An uncertainty that remains, however, is the degree to which the values of the morphological parameters (z_F, z_R, and z_W), the carbon-allocation parameters ($\overline{\eta}$ and ξ), and the aboveground fractions (γ or γ_1 and γ_∞) vary among locations. Valentine et al. (1994) compared an estimate of z_F for loblolly pine in Virginia and North Carolina that was based on a sampling of trees in 1991 and with an estimate of z_F for central Louisiana that was based on a sampling in 1992. These estimates were not significantly different, but this result can not be generalized. Suffice it to say that accurate measurements and characterizations of the variability of the parameter values are incomplete.

As stated at the outset, many empirical models of the growth and yield of even-aged stands are driven by height-growth models or are scaled by site index, I. The metabolic height-growth model makes it possible to use these existing empirical models to insinuate the effects of CO_2 fertilization and altered climates on stand growth and yield. However, such analyses should be undertaken with caution. Models that use I as a scaling parameter do so under an assumption that a particular value of I defines a fixed time-course of dominant tree height. The metabolic height-growth model would provide a new value of I given the reality of the increasing CO_2 concentration, but most of the response of height growth to increasing CO_2 may come after the index age. Therefore, the projections of the effects of the increasing CO_2 on stand growth and yield, as scaled by the new value of I, may understate the true effects. Growth-and-yield models that are driven by height-growth equations may be better choices for these types of projections.

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